

No. 5 — *Silicified Middle Ordovician trilobites:*
The Odontopleuridae

By

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CONTENTS

	<i>Page</i>
INTRODUCTION AND ACKNOWLEDGEMENTS	159
TERMINOLOGY	160
STRATIGRAPHICAL OCCURRENCE AND LOCALITIES	162
PART I: MORPHOLOGY, ONTOGENY AND EVOLUTION	166
Morphology of holaspid exoskeleton	166
Cephalon	166
Thorax	173
Pygidium	175
External surface	175
Abnormal specimens	178
Ontogeny	178
Locus of segmental divisions	182
Mode of life	185
Origin and evolution	186
PART II: SYSTEMATIC DESCRIPTIONS	193
Family Odontopleuridae Burmeister	193
Discussion of systematics of Odontopleuridae	194
Subfamily Odontopleurinae Burmeister	195
<i>Odontopleura</i> Emmrich	196
<i>Primaspis</i> R. and E. Richter	198
<i>P. ascitus</i> n. sp.	199
<i>Leonaspis</i> R. and E. Richter	205
<i>Diacanthaspis</i> Whittington	207
<i>D. cooperi</i> Whittington	211
<i>D. lepidus</i> n. sp.	216
<i>D. secretus</i> n. sp.	220
Discussion of ontogeny of <i>Diacanthaspis</i>	224
<i>D. ulrichi</i> n. sp.	225
<i>D. aff. ulrichi</i> n. sp.	228
<i>D. orandensis</i> n. sp.	228
<i>D. scitulus</i> n. sp.	230

	<i>Page</i>
<i>Acidaspis</i> Murchison	232
<i>Dudleyaspis</i> Prantl and Přibyl	234
<i>Radiaspis</i> R. and E. Richter	235
Subfamily Miraspinæ R. and E. Richter	235
<i>Miraspis</i> R. and E. Richter	236
? <i>M.</i> sp. ind.	238
<i>Ceratocephala</i> Warder	238
<i>C. laciniata</i> Whittington and Evitt	239
<i>C. rarispina</i> n. sp.	242
<i>C. (Ceratocephalina)</i> n. subgen.	243
<i>C. (C.) tridens</i> n. sp.	244
<i>Proceratocephala</i> Prantl and Přibyl	247
<i>Whittingtonia</i> Prantl and Přibyl	248
<i>Dicranurus</i> Conrad	248
Notes on other miraspinid genera	248
?Subfamily Miraspinæ R. and E. Richter	250
Odontopleurid protaspis	250
Subfamily Apianurinae n. subfam.	252
<i>Apianurus</i> n. gen.	252
<i>A. barbatus</i> n. sp.	254
Specimens at localities 2 and 3 differing from	
<i>A. barbatus</i> n. gen., n. sp.,	265
<i>A. glaber</i> n. sp.	268
<i>A.</i> sp. ind.	269
<i>A.</i> aff. <i>furcata</i> Linnarsson	270
<i>Calipernurus</i> n. gen.	271
<i>C. insolitus</i> n. sp.	273
Subfamily Selenopeltinae Corda	279
<i>Selenopeltis</i> Corda	279
Other genera, subgenera and species sometimes re-	
ferred to Odontopleuridae	282
REFERENCES	283
EXPLANATION OF PLATES 1-24	289

ILLUSTRATIONS

Plates

Plate

1. *Primaspis ascitus* n. sp.

Plate

2. *Primaspis ascitus* n. sp.
3. *Diacanthaspis cooperi* Whittington
4. *Diacanthaspis lepidus* n. sp.
5. *Diacanthaspis lepidus* n. sp.
6. *Diacanthaspis secretus* n. sp.
7. *Diacanthaspis secretus* n. sp. and *D. lepidus*
n. sp.
8. *Diacanthaspis ulrichi* n. sp.
9. *Diacanthaspis* aff. *ulrichi* n. sp. and *D. cooperi*
Whittington
10. *Diacanthaspis orandensis* n. sp.
11. *Diacanthaspis orandensis* n. sp. and *D. cooperi*
Whittington
12. *Diacanthaspis scitulus* n. sp.
13. *Diacanthaspis scitulus* n. sp.
14. *Miraspis* sp. ind. and *Ceratocephala laciniata*
Whittington and Evitt
15. *Ceratocephala rarispina* n. sp. and *C. (Cerato-*
cephalina) n. subgen., sp. ind.
16. *Ceratocephala (Ceratocephalina) tridens* n.
subgen., n. sp.
17. *Apianurus barbatus* n. gen., n. sp.
18. *Apianurus barbatus* n. gen., n. sp.
19. *Apianurus barbatus* n. gen., n. sp.
20. *Apianurus barbatus* n. gen., n. sp., and *A. aff.*
furcata Linnarsson
21. *Apianurus glaber* n. gen., n. sp., *Apianurus* n.
gen., sp. ind., and miraspinid ? protaspis
22. *Calipernurus insolitus* n. gen., n. sp.
23. *Calipernurus insolitus* n. gen., n. sp.
24. *Calipernurus insolitus* n. gen., n. sp.

Figures

Figure

Page

1. Notation for spines of Stage 0 cranidium 161
2. Hypostomes characteristic of subfamilies 171
3. Classification, relationships, range in time of
Odontopleuridae 188-189

Figure		Page
4.	<i>Odontopleura ovata</i> Emmrich	197
5.	<i>Primaspis primordialis</i> (Barrande)	198
6.	Development of <i>Primaspis ascitus</i> n. sp.	204
7.	<i>Leonaspis</i> n. sp.	206
8.	Age and comparison of species of <i>Diacanthaspis</i>	208-209
9.	Development of <i>Diacanthaspis cooperi</i> Whittington	213
10.	Reconstruction of <i>Diacanthaspis lepidus</i> n. sp.	218
11.	Development of <i>Diacanthaspis secretus</i> n. sp.	222
12.	Development of <i>Diacanthaspis ulrichi</i> n. sp.	227
13.	<i>Acidaspis brightii</i> Murchison	233
14.	<i>Dudleyaspis quinquespinosa</i> (Lake)	234
15.	<i>Miraspis mira</i> (Barrande)	237
16.	<i>Ceratoccephala laciniata</i> Whittington and Evitt	239
17.	<i>Whittingtonia bispinosa</i> (M'Coy)	247
18.	<i>Dicranurus monstrosus</i> (Barrande)	249
19.	Reconstruction of <i>Apianurus barbatus</i> n. gen., n. sp.	253
20.	Cephalon of <i>Apianurus barbatus</i> n. gen., n. sp.	256
21.	Triangular graph of dimensions of <i>Apianurus barbatus</i> n. gen., n. sp.	259
22.	Development of <i>Apianurus barbatus</i> n. gen., n. sp.	261
23.	Triangular graph of dimensions of <i>Apianurus barbatus</i> n. gen., n. sp., and <i>Calipernurus insolitus</i> n. gen., n. sp.	272
24.	Reconstruction of <i>Calipernurus insolitus</i> n. gen., n. sp.	274
25.	<i>Selcnopeltis buchi</i> (Barrande)	281

Tables

Table		Page
1.	Numbers of exoskeletal parts of two species of <i>Diacanthaspis</i> at localities 2-4	217
2.	Numbers of exoskeletal parts of three species of <i>Diacanthaspis</i> at locality 8	229
3.	Numbers of odontopleurid cranidia at locality 8	242
4.	Numbers of exoskeletal parts of all sizes of <i>Apianurus</i> n. gen., and <i>Calipernurus</i> n. gen.	267

INTRODUCTION AND ACKNOWLEDGEMENTS

The photographs show the remarkable nature of the silicified material from Virginia — superbly preserved, free from the matrix, undistorted, and including adults and growth stages. These specimens afford a detailed picture of an early part of the history of odontopleurid trilobites, and thus throw new light on the morphology and evolution of the family. The best odontopleurid material previously known was that described by Barrande (1852, 1872) and recently re-studied by Prantl and Přibyl (1949). Although these Bohemian odontopleurids range in age from Ordovician to Devonian, they are not as well preserved, nor are growth stages known. It is my good fortune that the Museum of Comparative Zoology houses the Schary Collection (to which Barrande originally had access), for this circumstance enabled me to study the Bohemian species at first hand. A visit to Britain in 1953, and generous loans from American museums, have permitted me to see additional specimens. The type and certain other species have been described elsewhere (Whittington, 1956b), and two silicified species from Virginia were treated of by Whittington and Evitt (1954). In Part II of this paper the remainder of the silicified odontopleurids are described in detail. In Part I, the morphology, ontogeny, and evolution of the family are discussed in general terms. Part II embodies a classification arising out of the new data, and my views on evolution, and includes notes on all the genera which have been referred to the Odontopleuridae.

The amount of morphological detail which the silicified exoskeletons reveal enables fine distinctions to be drawn between genera and between species, i.e. it encourages "splitting." Examples are the new subgenus *Ceratocephala* (*Ceratocephalina*), the differences between *Apianurus* n.gen. and *Calipernurus* n.gen., and between some of the species of *Diacanthaspis*. On the other hand, the seven species of *Diacanthaspis* seem to form part of a natural, related group, and I have widened the original diagnosis of *Diacanthaspis* rather than split it into subgeneric groups. In dealing with the less well-preserved and often incomplete material on which some Ordovician and all later genera have been established, I have tended to "lump" rather than

"split." Thus, widely varying degrees of morphological difference separate the genera shown in Text-figure 3, and these differences are not of equal rank.

Dr. G. Arthur Cooper and his colleagues at the U. S. National Museum first discovered silicified trilobites in the Middle Ordovician limestones of Virginia about 1935. In succeeding years a large collection was prepared, and in 1946 Dr. Cooper invited me to study it, under project grant 491-46 from the Penrose Bequest of the Geological Society of America. Meanwhile, Dr. William R. Evitt, University of Rochester, independently discovered these fossils, and since 1947 he and I have collaborated in the preparation of additional material and in studies of it. The silicified trilobites here described are thus derived from our own as well as U. S. National Museum collections. A special debt of gratitude is owed to Mrs. Evitt for her painstaking sorting of the finest residues, which brought to light many of the tiny growth stages. I am also grateful to Mrs. Stanley J. Olsen, Mrs. Robert E. Kay, and Mr. Ira B. Laby for preparing the enlargements from my negatives and for aiding in mounting the plates. Text-figures 10 and 19 were drawn from my sketches by Mr. F. Y. Cheng, the remainder by Miss Pat Washer. Professor L. Størmer, Paleontological Institute, Oslo, kindly permitted me to describe a Norwegian species here.

TERMINOLOGY

The terminology used herein is the same as that employed by Whittington and Evitt, 1954, pp. 11-14, with certain additions and emendations:—

Cephalic spines: to simplify description of cephalic spines a system of letters and numbers has been adopted (Text-fig. 1). Median or paired *arial spines* of the glabella have been numbered 1-5, commencing with the median occipital and numbering forwards; 2a is an additional pair appearing later in the ontogeny than 1 and 2. These numbers do not correspond with those used by Whittington and Evitt (1954, text-fig. 16), where 2a is numbered 2, 2 is 3, 3 is 4, etc. Certain *paired cheek spines* have been lettered as shown. In the protaspis and Stage 0 cephalo of *Diacanthaspis* (Text-figs. 9, 11, 12) and *Apianurus* n. gen. (Text-fig. 22) there is a long, backwardly-directed spine

at the extremity of the posterior border of the fixed cheek, as well as a long spine on the border of the free cheek. These spines have been called *fixigenal* and *librigenal* respectively (terms proposed by Richter, 1932), in preference to the older terms metacranial and parial of Raw (1925).

Antennular notch: a notch in the margin of the free cheek immediately outside the anterior branch of the facial suture (*a* in Text-fig. 20; see also Pl. 1, figs. 2, 5; Pl. 17, figs. 7, 10). As

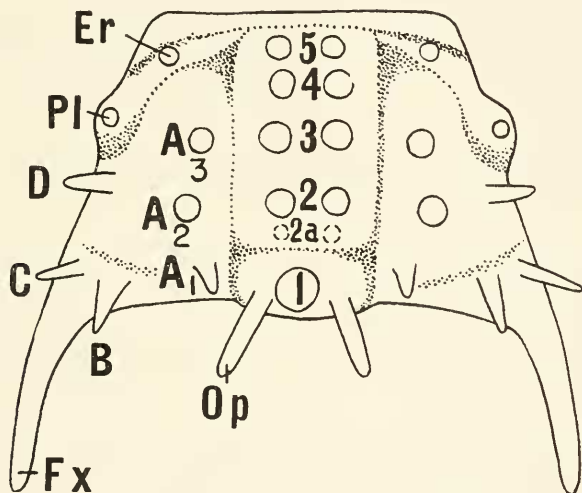


Figure 1. Cranidium of Stage 0 odontopleurid based on that of *Apianurus barbatus* n.gen., n.sp., with paired spines numbered and lettered as follows: 1, 2a, 2, 3, 4, 5, six pairs of axial glabellar spines numbered forward from the occipital ring; A₁, A₂, A₃, on fixed cheek; B, C, on posterior border; D, on fixed cheek behind palpebral lobe; Er, on eye ridge; Fx, fixigenal; Op, paired occipital spine; Pl, on summit of palpebral lobe.

explained under "Cephalon: hypostome" and "Mode of Life," this notch may permit the antennule to protrude forward when the animal is resting on the sea bottom.

Pleural spines: The pleura may be divided by a pleural furrow into a convex anterior and posterior band, and each of these bands may be prolonged distally into a spine (the anterior into more than one spine), here called *anterior pleural* (not terminal

of Prantl and Přibyl, 1949, p. 128) and *posterior pleural* spines respectively.

Pleural region is used for that part of the pygidium outside the axis, rather than pleural lobe.

Pygidial spines: Commonly one paired spine is longer and stouter than the others, and is here called the *major* spine; it may arise from the border or the surface of the pleural region, and the base is always connected to the first axial ring by a low ridge, here termed the *pleural ridge*.

Sagittal (*sag.*), *Exsagittal* (*exs.*), and *Transverse* (*tr.*) refer respectively to the median line, a line parallel to, but outside of the median, and a direction at right angles to the median. The abbreviations used in the text are given in parentheses.

STRATIGRAPHICAL OCCURRENCE AND LOCALITIES

The specimens described here were obtained from limestones of the Edinburg, Oranda and Martinsburg formations of the Shenandoah Valley, northern Virginia. The stratigraphy of these formations has been described by Cooper and Cooper (1946), and the classification and correlation is summarized in Twenhofel *et al.* (1954). Trilobites from the Edinburg and underlying limestones have been described by Evitt (1951), Cooper (1953), and Whittington and Evitt (1954), and the latter work also contains an account of the mode of occurrence, preservation, and method of extraction of the silicified specimens. Trilobites from the lower Martinsburg formation have been described by Whittington (1941), Evitt (1953) and Evitt and Whittington (1953). Odontopleuridae first appear in the lower Lincolnshire limestone (*Ceratocephala triacanthæis* Whittington and Evitt and fragments of *Apianurus* n. gen.), below the Edinburg formation. In the lowest part of the latter formation (localities 2-4) they are abundant and exhibit the greatest variety. In the slightly higher horizon at locality 6 odontopleurids are rare, but they become numerous and varied again some 400 feet higher in the section in the Oranda formation. The latter is not more than 50 ft. thick, and in the lowest part of the succeeding Martinsburg formation silicified odontopleurids again occur in fair abundance and variety. Not all the blocks of

limestone collected yield good material, and the same species do not appear at different localities in the same formation — perhaps because of slight differences in horizon. Thus *Diacanthaspis ulrichi* n. sp. is the only odontopleurid at the lower Edinburg locality 7, is rare at locality 4, and unknown at 2 and 3. *Primaspis ascitus* n. sp. is only known at locality 10 in the lower Martinsburg, and does not accompany *D. cooperi* at localities 9, 11 and 12.

The localities (cf. Whittington and Evitt, 1954, pp. 5-6) and the odontopleurids obtained at each are listed below. Tables 1-4 give numbers of specimens recovered of particular species.

Edinburg limestone

Locality 2 — Lower part of Edinburg limestone (bed 18 of Cooper and Cooper, 1946, geologic section 19, pp. 94-95), yellowish-weathering argillaceous limestone forming edge of quarry and along strike of same bed, in field between quarry and railroad; just north of railroad tracks at switch a quarter of a mile east of Strasburg Junction, just west of Strasburg, Shenandoah County, Virginia. Some of the finest specimens illustrated here came from blocks collected at this locality and prepared by Dr. G. Arthur Cooper.

Diacanthaspis lepidus n. sp.

Diacanthaspis secretus n. sp.

Ceratocephala laciniata Whittington and Evitt, 1954

Apianurus barbatus n. gen., n. sp.

Apianurus glaber n. gen., n. sp.

Apianurus sp. ind.

Calipernurus insolitus n. gen., n. sp.

Locality 3 — Lower part of Edinburg limestone, section in field on south side of road, 0.2 mile east of Strasburg Junction, just west of Strasburg, Shenandoah County, Virginia. The section dips about 38° SE. The lowest beds were 6 feet of granular limestones with *Girvanella* sp., about 91 feet from the east edge of the quarry dump at the top of the field. These may be upper Lincolnshire limestone. About 20 feet stratigraphically higher, alternations of dark granular limestone and dark fine-grained limestone with sponge spicules were seen. These beds seem to be

the basal Botetourt limestone member of the Edinburg formation (Cooper and Cooper, 1946, p. 80), and blocks from them were collected and prepared by Dr. G. Arthur Cooper, Dr. and Mrs. W. R. Evitt, and Whittington. These yielded all the species known from locality 2 except *Apianurus* sp. ind. In addition *Miraspis* sp. ind. and *Ceratocephala* (*Ceratocephalina*) *tridens* n. subgen., n. sp., occur.

Locality 4 — Botetourt member, lower part of Edinburg limestone, in upper part of field northeast of Virginia State Highway 639, at a point 0.25 mile from its junction with U.S. Highway 11. This junction is 0.7 mile southwest of Strasburg, Shenandoah County, Virginia. The outcrop is approximately half a mile southwest of locality 3 along the strike of the beds. Collected and prepared by Dr. and Mrs. W. R. Evitt and by Whittington. and notable for yielding some of the finest tiny specimens.

Diacanthaspis lepidus n. sp.

Diacanthaspis secretus n. sp.

Diacanthaspis ulrichi n. sp.

Ceratocephala laciniata Whittington and Evitt, 1954

Ceratocephala (*Ceratocephalina*) *tridens*, n. subgen., n. sp.

Apianurus barbatus n. gen., n. sp.

Apianurus glaber n. gen., n. sp.

Locality 6 — Edinburg limestone, lower part, Hupp Hill, at entrance to Battlefield Crystal Caverns, and in field on opposite (east) side of U. S. Highway 11, about 1½ miles north of Strasburg, Shenandoah County, Virginia. Discovered by Dr. G. Arthur Cooper, later collections by Whittington. Odontopleurids are rare, only one or two parts of exoskeletons of the following being known:—

Diacanthaspis secretus n. sp.

Ceratocephala laciniata Whittington and Evitt, 1954

Apianurus barbatus n. gen., n. sp.

Locality 7 — Lower part of Edinburg limestone, 300 feet ± south 40° east of bridge, 1¼ miles east of Edinburg, Shenandoah County, Virginia. Originally collected by E. O. Ulrich, later (1931) by Charles Butts, and yielding only one odontopleurid, *Diacanthaspis ulrichi* n. sp.

Oranda formation

Locality 8 — Lower 5 feet of formation, cobbly limestone, in bank and pasture on north side of Virginia secondary highway 777, just west of its junction with Virginia secondary highway 910, and *circa* 300 yards north of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia. Discovered by G. Arthur Cooper, later collections by Cooper and A. R. Loeblich, Jr., W. R. Evitt, and Whittington.

Diacanthaspis orandensis n. sp.

Diacanthaspis scitulus n. sp.

Diacanthaspis aff. *ulrichi* n. sp.

Ceratocephala rarispina n. sp.

Apianurus barbatus n. gen., n. sp.

Martinsburg shale

Locality 9 — Road cut, gutter, and loose blocks in pasture on west side of Virginia secondary highway 910, about half a mile north of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia. Same as locality 1 of Evitt and Whittington, 1953, p. 55. Collected and prepared by Dr. and Mrs. W. R. Evitt, Dr. G. Arthur Cooper, and Whittington.

Diacanthaspis cooperi Whittington, 1941

Locality 10 — Pasture on north side of Virginia secondary highway 772, about 1 mile east of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia. Collected and prepared by Dr. and Mrs. W. R. Evitt.

Primaspis ascitus n. sp.

Diacanthaspis cooperi Whittington, 1941.

Locality 11 — Loose blocks in pasture on north side of Virginia secondary highway 616, $\frac{1}{4}$ mile east of intersection with Virginia secondary highway 699, and $2\frac{1}{2}$ miles north-northeast of Spring Hill, 7 miles north of Staunton, Augusta County, Virginia. The Oranda formation immediately underlies the lower Martinsburg formation and outcrops a short distance to the west. The locality is that from which all the material described by me (including *Diacanthaspis cooperi*) in 1941 came. At that time (Whittington, 1941, p. 492) two localities were given, distant respectively $2\frac{1}{2}$ miles north-northeast, and 3 miles north-northeast, of Spring

Hill and Long Glade. Spring Hill is a new name for the settlement formerly called Long Glade, and the confusion probably arose because the blocks of limestone were collected at different times (cf. Evitt, 1953, p. 34). The first blocks were collected by Dr. G. Arthur Cooper, later ones by Cooper and Whittington.

Locality 12 — In field on south side of Virginia secondary highway 753, 1 mile west of intersection with Virginia secondary highway 732, and 3½ miles north-northeast of Spring Hill, Augusta County, Virginia. This locality, visited by Dr. G. Arthur Cooper and Whittington, is one mile northeast of locality 11, and yields *Diacanthaspis cooperi*.

PART I: MORPHOLOGY, ONTOGENY AND EVOLUTION

Morphology of Holaspid Exoskeleton

The family diagnosis (p. 193) epitomises the morphology of an odontopleurid, and in this section certain aspects are commented on more fully, these being chiefly features on which I have information additional to that available to Prantl and Přibyl (1949).

Cephalon

Attitude: The characteristic attitude of the strongly convex cephalon is discussed below under "Mode of Life." The convexity of the cephalon and its position relative to the thorax and pygidium were recognized by some earlier authors (e.g. Weller, 1907, Pl. 23, figs. 1-4; Warburg, 1933, p. 9, footnote; see also Whittington and Evitt, 1954, p. 54), but not, apparently, by Barrande. Many of Barrande's drawings were made from specimens flattened in shale or calcareous mudstones, and show an exterior view of the cephalon combined with a dorsal view of thorax and pygidium (for definitions of these terms see Whittington and Evitt, 1954, p. 11). The present reconstructions attempt to remedy this situation (compare Text-figs. 4, 15, 25 with Barrande, 1852, Pl. 39, figs. 33, 1; Pl. 37, fig. 25, respectively).

Occipital ring: Conspicuous in odontopleurids is the way in

which the antero-lateral portion of the occipital ring merges with the inner posterior corner of the cheek. Behind this region the posterior border is distinctly separated from the remainder of the occipital ring, and the axial furrow more or less well developed, as it is beside the lateral glabellar lobes. The occipital ring in most odontopleurid genera is strongly convex and commonly elongated so that it projects behind adjacent parts of the posterior border. As Prantl and Přibyl pointed out (1949, p. 127), a median occipital tubercle is always present, and a median spine or paired spines may also be developed. The species of *Diacanthaspis* here described (Text-fig. 8) show that the median tubercle, or paired spines, or both may be greatly enlarged, or none may be especially prominent, in a group of closely related species. In genera such as *Ceratocephala* and *Miraspis* (Text-fig. 15), where long, stout, paired occipital spines are developed, a posterior occipital band, below and behind the bases of these spines, is developed (cf. Warburg, 1933). Such a band is, however, not present in *Acidaspis* (Text-fig. 13) or *Dicranurus* (Text-fig. 18), though the median (in the former) and paired (in the latter) occipital spines are large. The view of Reed (1925, p. 420) that the posterior occipital band represents the occipital ring, and that the part in front belongs to the glabella, has been adequately refuted by Warburg (1933) and Öpik (1937, pp. 45-47).

Where I have been able to observe both surfaces of the exoskeleton, as in *Primaspis ascitus*, n. sp. (Pl. 1, figs. 1, 6), the occipital lobes are small, gently convex, subcircular in outline, situated immediately behind the deep outer part of the occipital furrow. Their convexity, rather than any distinct furrow, separates them from the rest of the occipital ring inside and behind them, and they are indistinctly bounded posteriorly. On the inner surface they are seen to be in front of the outer part of the doublure of the occipital ring. In structure and position they are analogous to the lateral glabellar lobes, though they do not extend back to the posterior margin of the segment, and are much less distinct than the first and second glabellar lobes. In *Ceratocephala laciniata* and *C. triacanthcis* (Whittington and Evitt, 1954, Pl. 6, fig. 4; Pl. 8, figs. 1, 2; Pl. 25, figs. 10, 11) occipital lobes are scarcely distinguishable, whereas in certain

younger species of the same genus (e.g. Warburg, 1933, text-figs. 2, 3) the outer part of the occipital ring, between the occipital furrow and posterior band, is inflated. Similarly, in *Dicranurus hamatus* (Whittington, 1956b, Pl. 60, figs. 11, 12) the inflation of the antero-lateral part of the occipital ring, though vaguely defined, especially postero-laterally, is greater than in *D. monstrosus* (Text-fig. 18). Species of other genera show the same features, and indicate that, when occipital lobes are developed (they are absent altogether in some genera and absent in certain species only of other genera), they are situated in the antero-lateral corner of the occipital ring, probably outside the margin of the doublure, and ill-defined on the posterior and inner sides. Their variability suggests that presence or absence of such lobes can scarcely be used as a generic character.

Glabellar lobes and furrows: Two pairs of lateral glabellar lobes are always present, the first (basal) pair the larger, and, except in a few genera and certain species of other genera, small, variably-developed, third lateral lobes are present. Particularly in *Ceratocephala* and *Miraspis* the third lobes are small and depressed, and have been regarded as not developed by Prantl and Příbyl (1949, pp. 180, 194). The convexity of the lateral lobes and degree of their separation from the median glabellar lobe are variable (contrast, for example, *Leonaspis*, Text-figure 7, with *Whittingtonia*, Text-figure 17), and in *Apianurus* n.gen. and *Primaspis keyserlingi* (Barrande, 1852, Pl. 36, figs. 10, 12) the lateral lobes are fused. The peculiarities of the glabellar lobation of *Selcnopeltis* (Text-fig. 25) set it apart. The frontal lobe varies in width, sometimes being only as wide as the median lobe (*Acidaspis*, Text-fig. 13) but usually it is expanded to extend in front of the second or third lobes (*Leonaspis* n. sp., Text-fig. 7; *Dicranurus hamatus*, Whittington, 1956b, Pl. 60, fig. 15; *Miraspis mira*, Text-fig. 15). The eye ridge terminates opposite the lateral extremity of the frontal lobe, and may merge into it (*Ceratocephala*, see Whittington and Evitt, 1954, Pl. 9, fig. 2) or be separated from it by a low depression, the axial furrow (*Primaspis ascitus* n. sp., Pl. 1, figs. 2, 5). Hupé's diagram (1953, p. 102, text-fig. 62; repeated in 1955, p. 236, text-fig. 205) conveys a misleading impression, in that figure 62 (1), showing 3 pairs of lateral glabellar lobes, is labelled "primitif"

and "normale," and figure 62 (3) with 2 pairs of lateral lobes. is labelled as showing "regression progressive et complète" of the fourth segment (from the posterior margin). In fact no such progressive reduction occurs, for genera with 2 and 3 pairs of lateral lobes appear at about the same time (*Diacanthaspis*, *Primaspis*, and *Ceratocephala*), and *Ceratocephala* and *Dicranurus*, both having 3 pairs of lateral lobes. are known in the Middle Devonian.

The outer part of the occipital furrow, and each glabellar furrow (especially at the inner end), is deepened and forms a strong ridge on the inner surface (Pl. 1, fig. 6; Pl. 5, fig. 4; Pl. 7, fig. 5; Pl. 12, fig. 7; Pl. 15, fig. 5; Pl. 20, fig. 11; Pl. 21, fig. 6; Pl. 22, fig. 6). The quartz along the crests of these ridges may appear darker, strengthening the impression that these ridges are points of muscle attachment. So far as is known, however, these thick ridges are not extended as ventral processes. The outer part of articulating and ring furrows is similarly deepened (e.g. Pl. 12, figs. 6, 18) but does not form so strong a ridge on the inner surface.

Eye lobe, eye ridge, facial sutures: The external covering of the eye of *Ceratocephala* has been described (Whittington and Evitt, 1954, p. 16) as having the outer surface smooth or faintly divided into numerous closely spaced, slightly raised facets, the inner surface showing shallow pits similarly arranged. The external covering of the eye of the silicified specimens of other genera described here appears to be similar, the facets on the outer surface sometimes clearly delineated (Pl. 2, figs. 18, 22; Pl. 3, fig. 21; Pl. 16, fig. 23; Pl. 17, fig. 21; Pl. 23, figs. 9, 10). This type of eye surface seems to be typical of odontopleurids.

The presence of the eye ridge, and of sutural ridges (Whittington and Evitt, 1954, pp. 13, 17-19), notably where the suture approaches either border, is characteristic.

Fusion of the facial sutures, presumably a secondary phenomenon, has been suggested as a criterion for distinguishing genera of odontopleurids. It is true that in some specimens in which the exoskeleton is preserved it is almost impossible to detect the course of the suture, but whether or not this means that secondary fusion has taken place is difficult to determine. In any event this single character is not regarded as a reliable

criterion upon which to base a genus (Whittington and Evitt, 1954, p. 53).

Librigenal spine: Prantl and Přibyl (1949, pp. 126, 131, etc.) stated that, in *Selenopeltis* and miraspinids, the librigenal spine arose from the "surface of the cheeks above the genal angle," rather than being a backward and outward extension of the rolled borders, at the genal angle, as it is in odontopleurinids. In *Ceratocephala* (Whittington and Evitt, 1954, Pl. 6, fig. 17; Pl. 25, figs. 12-14), the broad base of the librigenal spine merges into the upper surface of the posterior and lateral borders and the sutural ridge. In *Ceratocephala* (*Ceratocephalina* n. subgen.) (Pl. 16, figs. 23, 24) it likewise arises from the upper surface of the border, and a line of spines on the margin of the border is continuous below it. The fact that the doublure extends beneath the base of the librigenal spine (Pl. 16, fig. 9) shows that the spine arises from the border and not the surface of the cheek (cf. Whittington and Evitt, 1954, p. 52). Thus I do not agree with Prantl and Přibyl (1949, p. 131, etc.) that the miraspinid librigenal spine arises in a way that is fundamentally different from, and originates from other cephalic segments than, that of odontopleurinids. I believe rather that the difference between the librigenal spines in the two subfamilies is one of direction and not place of origin. In apianurineids the librigenal spine also arises from the cephalic border, but from a point farther forward. The ontogeny of *Diacanthaspis*, of *Apianurus* n. gen., and of *Ceratocephala* shows that the librigenal spine develops in much the same way in each group, but does not show to which cephalic segment it may belong.

Hypostome: The hypostomes of a species of *Primaspis* and those of *Apianurus* n. gen. and *Calipernurus* n. gen. are described here, and others in Whittington, 1956b. Thus the hypostomes of more than half of the odontopleurid genera are known, and seem to fall into four types, exemplified in Text-figure 2. The "family resemblance" between them is shown particularly by the small anterior wing (lacking the wing process), lateral notch and pointed shoulder, middle body with large depression in antero-lateral corner, from which the middle furrow runs inward and backward, and tiny posterior wing. The types distinguished form one of the main bases of the four subfamilies recognized.

Prantl and Přibyl (1949, p. 134, etc.) stressed the difference between the odontopleurininid and the *Selenopeltis-Ceratocephala* types of hypostome. The latter two present a considerable likeness, and in both the crescentic tip of the posterior lobe of the middle body is inflated and extends outside the depression in the antero-lateral corner of the middle body. In the odontopleurininid (and apianurininid) type the tip of the posterior lobe of the mid-

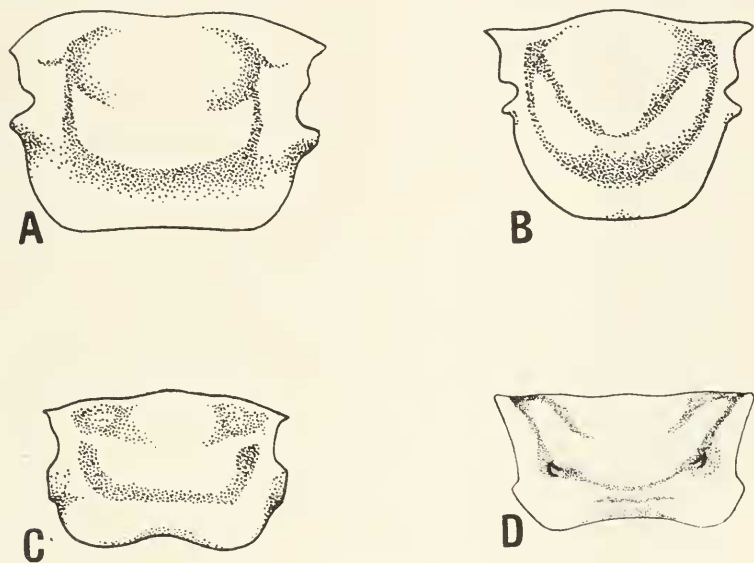


Figure 2. Hypostomes characteristic of each of the four subfamilies of Odontopleuridae. A, Odontopleurinae, *Primaspis*, based on that of *P. ascitus* n.sp. B, Apianurinae, *Apianurus*, based on that of *A. barbatus* n.gen., n.sp. C, Miraspiinae, *Ceratocephala*, based on that of *C. laciniata* Whittington and Evitt. D, Selenopeltinae, *Selenopeltis*, based on that of *S. buchi* (Barrande).

dle body does not extend as far forward. I hardly think this difference is as great as Prantl and Přibyl tend to make it by saying that in odontopleurininids the middle furrow starts from the lateral border furrow, whereas in *Selenopeltis* and *Ceratocephala* it starts from the anterior border furrow.

The silicified specimens of hypostomes have shown the exist-

ence of a circular hole through the doublure (Pl. 3, figs. 9, 10; Pl. 10, figs. 21, 24; Pl. 13, figs. 9, 11; Pl. 14, fig. 12; Pl. 23, fig. 15), situated on or near the sharp flexure associated with the shoulder. This hole is seen in species belonging to several genera, but is not exhibited by all species of a single genus—for example, *Diacanthaspis*. A similar-appearing opening in the cephalic and thoracic doublure of other trilobites is the Panderian opening, but whether or not this similarity implies that they are analogous structures is uncertain.

The macula is not discernible in the odontopleurid hypostomes here studied, except perhaps as the smooth area at the inner end of the middle furrow of *Primaspis ascitus*, n. sp. (Pl. 1, fig. 20). The depression in the antero-lateral corner of the middle body is conspicuous, however, in that it is smooth on the external surface, and the quartz is often differently coloured, and on the inner surface there may be some exfoliation. Thus it resembles the similarly-situated area in *Sphaerexochus* (Whittington and Evitt, 1954, p. 25) and may be an area of muscle attachment.

The problem of the manner in which the hypostome is attached in odontopleurids has been discussed previously (Whittington, 1941, p. 516; Whittington and Evitt, 1954, pp. 20, 55-56). Isolated rostra of the silicified species have not been found, but the unique specimen of *Acidaspis cincinnaticnsis* recently described (Whittington, 1956b) has the rostrum in place. The posterior edge of this rostrum is straight (except distally where it curves to meet the inner edge of the cheek doublure), and obscurely bevelled in this specimen. Measurement shows that the straight edge fits exactly against the straight, bevelled, anterior edge of the hypostome. The fit of the bevelled edges suggests that the hypostome lies approximately in the horizontal plane (on the orientation adopted here), or slopes slightly downward and backward. The tip of the small anterior wing lies beneath the intersection of the axial and preglabellar furrows, just in front of the eye ridge. This intersection, and the border furrow just outside it, is usually deepened in odontopleurids, though it does not form a large projection on the inner surface. Thus the attachment of the hypostome seems to be as previously suggested—at the suture and with a muscular link between anterior wing and/or pit at anterolateral corner of the middle body to

unspecified point or points on cranium. One of the latter is perhaps the prelabellar furrow and border furrow outside the inner end of the eye ridge (i.e. about where the anterior boss is in other trilobites). The hypostome of *Apianurus barbatus* n. gen., n. sp., is restored in approximately this position in Text-figure 20. This attachment appears not to have been as rigid as that in cheirurids and allied families (Whittington and Evitt, 1954, pp. 19-21), and the evidence cited by Prantl and Přibyl (1949, p. 196) of many specimens of *Miraspis mira* in which the hypostome is preserved but rotated through 180° and lying just in front of the cephalic margin, is interpreted by them as indicating an "easily movable connection." However, the flat surfaces that are apposed along the hypostomal suture are not suggestive of movement at the suture having been possible during life.

Antennular notch: Figures 5, 7, of Plate 17 show that there is a conspicuous notch in the anterior cephalic border immediately outside of where the connective suture crosses the border. It has previously been argued (Whittington and Evitt, 1954, p. 20) that the antennule is attached to the surface of the anterior boss and passes through the lateral hypostomal notch. It may also have passed through the notch (here called the antennular notch) in the anterior cephalic border, which would have permitted the antennule to be forwardly extended, when the cephalic margin was resting on the sea bottom, in the manner suggested under "Mode of Life." The antennular notch is developed to a greater or lesser extent in most odontopleurids (e.g. Pl. 1, figs. 2, 5; Pl. 12, fig. 2; Pl. 22, figs. 3, 6).

Thorax

The eight thoracic segments of *Leonaspis* n. sp. (Whittington, 1956b) are unusual, nine or ten being most commonly seen in the family. The backwardly-convex curve of the posterior margin of the prominent axial ring (and the occipital ring) is complemented by the curve of the articulating furrow. Medially, the ring adjacent to this furrow is less elevated. The articulating half ring is long (sag.), particularly that of the first segment. In some species and genera the antero-lateral part of the axial ring is inflated, e.g. *Selenopeltis* (Text-fig. 25), *Miraspis* (Text-

fig. 15), and *Proceratocephala* (Whittington, 1956b, Pl. 60, figs. 2, 10). A posterior band of the type seen on the occipital ring in some genera has not been seen on axial rings.

The horizontal pleurae may be unfurrowed as in *Apianurus* n. gen. (Pl. 18, figs. 6, 9) and *Ceratocephala* (Whittington and Evitt, 1954, Pl. 8, fig. 10), but are generally divided by the straight, transverse pleural furrow into a narrow anterior and wider (exs.) posterior band. The narrow, raised ridge of the posterior pleural band of *Selenopeltis*, with its strong curve convex forward, is distinctive. A posterior flange is present in many species. At the fulcrum the pleural bands are continued by spines: a stout, more or less horizontal, posterior spine, and one or more slimmer, shorter, anterior spines, downwardly directed. The doublure is curled under at the base of these spines, and forms the fulcral articulating socket and process. In odontopleurinid genera the broad-based librigenal spine is directed horizontally outward and backward beside the thorax, and consequently the first two or three thoracic pleurae are faceted so that they fit beneath the posterior cephalic border and librigenal spine. Thus the anterior pleural spine is absent, and the posterior pleural spine short (e.g. Pl. 3, fig. 11; Pl. 8, fig. 12). The anterior pleural spines of the third or fourth, and successive, segments are present and the posterior pleural spine is long and backwardly directed. In miraspinids (Text-figs. 15, 18) and apianurids (Text-fig. 19), however, the librigenal spines are respectively directed upwardly, and situated far forward on the cephalon, and no faceting and truncation of the thoracic pleural terminations is necessary to permit fitting behind the cephalon. Thus the posterior pleural spines are successively directed obliquely forward, outward, and obliquely backward. This difference in development and direction of pleural spines has been regarded by Prantl and Přibyl (1949) as indicating a distinction of family rank between odontopleurinids and miraspinids, but hardly seems to be of this magnitude (cf. Whittington and Evitt, 1954, p. 52). Likewise the "stunting" of the first two or three thoracic segments hardly seems an adequate basis for the subgenus *Leonaspis* (*Kettncraspis*) Prantl and Přibyl (1949, p. 165; see Whittington, 1956b).

An inflation of the posterior pleural band at the fulcrum

characterises certain odontopleuriniids, e.g. *Primaspis* (Pl. 1, figs. 11-14), some species of *Leonaspsis*, and *Acidaspsis* (Whittington, 1956b) and may indicate relationship.

Pygidium

Major border spines, i.e. one notably larger pair among the several arising from the pleural regions, are characteristic, but may not be developed at all (*Diacanthaspis secretus* n.sp., Pl. 7, fig. 10; *Radiaspis radiata*, see R. and E. Richter, 1917, text-fig. 10) or only slightly developed, as in some species of *Ceratoccephala* (Barrande, 1852, Pl. 38, figs. 5, 18). When present, the major spine is connected at its base to the first axial ring by the pleural ridge which runs across the pleural region. Commonly, the major spine arises from the upper surface of the pygidial border, but may take its origin from inside the border of the pleural region (e.g. *Diacanthaspis orandensis* n.sp., Pl. 10, figs. 17-19; *Apianurus barbatus* n.gen., n.sp., Pl. 18, fig. 12; *Calipernurus insolitus* n.gen., n.sp., Pl. 24, figs. 27, 28). In this latter case it seems quite independent of the border spines, though the pleural ridge is present. When the major spine arises from the border it is commonly the third or fourth spine, and in *Miraspis* is unusually far forward on the border, though still the third spine (cf. Prantl and Přibyl, 1949, pp. 128-129). As remarked under "Locus of segmental divisions" the major spine and pleural ridge are homologous with the thoracic posterior pleural band and spine.

The doublure of the pygidium is curled under, not wide, and there is a small projection posteriorly, directed up toward the axis.

External Surface

Short, thorn-like spines, tubercles, and granules are characteristic; their form and arrangement are shown by the plates (cf. Whittington and Evitt, 1954, Pls. 6-9, 25, 26). Rarely is the external surface everywhere smooth, as it seems to be in *Primaspis keyserlingi*, but commonly the deeper parts of furrows, and the doublure, are smooth. A symmetrical arrangement of the prominent spines, making transverse rows across the exoskeleton,

is typical of early developmental stages (see below) and may persist into the adult. In most adults this symmetry is less obvious, and may be lost altogether (e.g. *Primaspis ascitus*, Pl. 1, fig. 1). Conspicuous paired spines on axial rings are common, though rarely are they as large on the thoracic rings as in *Proceratocephala* (Whittington, 1956b, Pl. 60, figs. 2, 5, 10).

It was shown previously (Whittington and Evitt, 1954, pp. 56-59, text-fig. 1, etc.) that small openings occur on the distal side of tubercles scattered along occipital and librigenal spines, and at and near the tips of spines on the cephalic and pygidial border. Such openings are characteristic of the specimens described here (e.g. Pl. 7, figs. 12-14; Pl. 11, fig. 16; Pl. 13, fig. 14; Pl. 23, fig. 6; Pl. 24, figs. 21, 24). It was further suggested that in *Ceratocephala laciniata* there may have been a single opening, possibly occupied by a hair, at the tip of the thorn-like spines (Whittington and Evitt, 1954, p. 59; Pl. 8, fig. 11; Pl. 9, figs. 2, 4; text-fig. 1) scattered over the external surface of the cranidium. Among the few available cranidia of *C. varispina* n.sp., however, is one (Pl. 15, fig. 28) in which the thorn-like spines, where not obviously broken, are closed at the truncate tip by a plate in which there are minute depressions (appearing as dark spots in the photograph). The diameter of these depressions is less than that of some of the quartz grains replacing the exoskeleton, so that it is difficult to be sure of their nature. It seems probable that they are the orifices of canals through the exoskeleton. The thorn-like spines on the cranidium of *Diacanthaspis* are similar, sometimes showing an evenly cut off tip with a relatively large central opening (Pl. 7, fig. 15). A well-preserved specimen of *D. scitulus* n.sp. (Pl. 13, figs. 16, 17), however, has the truncated tip covered by a convex plate in which there are tiny depressions. These may show a regular arrangement of a central larger pit surrounded by smaller pits. A specimen of *D. lepidus* n.sp. (Pl. 4, fig. 22) shows a similar arrangement. In *D. cooperi* and *D. orandensis* n.sp. (Pl. 9, fig. 6; Pl. 11, fig. 19) the tip is slightly expanded and subspherical, with a large central depression or opening surrounded by smaller ones. In *D. aff. ulrichi* n.sp. (Pl. 9, figs. 7, 9) some spines show only a central opening, and others appear to show several openings. One may conclude that in *Diacanthaspis*, as in *C. varispina* n.sp.,

the tip of the thorn-like spines was pierced by one or more minute openings, but whether a hair issued from each opening is uncertain. The tubercles of *Primaspis ascitus* n.sp. (Pl. 2, fig. 21) appear to be closed at the summit, and in *Apianurus barbatus* n.gen., n.sp. (Pl. 18, figs. 19, 22) the characteristically curved tips of the thorn-like spines appear elosed.

In *Diacanthaspis lepidus* n.sp. (Pl. 5, fig. 1), *D. secretus* n.sp. (Pl. 6, fig. 22), and *D. ulrichi* n.sp. (Pl. 8, fig. 27) the tip of the librigenal spine is hooked. The hooked portion appears to be smooth, without openings, but proximally to the tip the usual type of opening is present. Such openings are numerous at the tip of the librigenal spines in species which do not have the hook (Pl. 13, fig. 14).

Tubercles on the external surface, as in *Primaspis ascitus* n.sp. or *Calipernurus insolitus* n.gen., n.sp., seem never to have had openings at the summit. The median occipital tubercle in both these species, however (Pl. 2, figs. 21, 23; Pl. 23, figs. 5, 7, 8), is larger than any other, and has four pits, arranged to outline a square (and rarely a faint, small, median pit) in its low, domed surface. It appears early in ontogeny (Pl. 2, figs. 6, 8; Pl. 24, fig. 1) and is retained in the largest holaspis known. The pits, appearing as dark spots, do not seem to be the openings of canals through the exoskeleton. The occipital doublure extends close underneath the tubercle and well in front of it in *P. ascitus* n.sp. (Pl. 1, fig. 6). No similar tubercle is seen on the axial rings of thorax or pygidium. The same type of median occipital tubercle has been observed in other species of *Primaspis*, in *Diacanthaspis cooperi* (Pl. 11, fig. 18), *D. ulrichi* n.sp. (Pl. 8, figs. 24, 30), *D. aff. ulrichi* n.sp. (Pl. 9, figs. 8, 9), *D. orandensis* n.sp. (Pl. 11, fig. 20), and *Leonaspis leonhardi* Barrande. This tubercle may be compared with the median glabellar tubercle of *Tretaspis seticornis* (Stormer, 1930, pp. 85-87, figs. 36, 37), which is similar but displays more clearly a fifth, centrally situated pit, as does the four-celled sense-organ of *Anaspides* (Hanström, 1934). Temple (1952, pp. 254, 258) has described the median occipital tubercle of protaspis and early meraspis stages of *Dalmanitina olini* as bearing five tiny tubercles, one central and the others forming a square. This may be an anala-

gous organ to that of the odontopleurids, but represented by tubercles rather than pits.

Hupé (1953, pp. 80-81) suggests that the median glabellar tubercle is the specialized homologue of median tubercles of succeeding segments, and this example in odontopleurids may represent such a specialization (presumably for some sensory function) of the median occipital tubercle.

Abnormal Specimens

Parts of exoskeletons showing marked deviation from the normal structure are rare, as they also seem to be in other collections of this type (cf. Ross, 1951, p. 134). The only examples among the present material are the single free cheek of *D. scitulus* n.sp. (Pl. 13, figs. 6, 7; the emargination apparently resulting from an injury) and the three pygidia of *Calipernurus insolitus* n.gen., n.sp. (Pl. 24, figs. 11, 17, 18, 20). As compared to the usual form (Pl. 24, fig. 27), these pygidia either lack one of the three posterior border spines, or have a single spine which bifurcates distally. This appears to be the result of abnormal growth rather than injury, and another specimen (Pl. 24, fig. 28) shows that even when three border spines are present, they may be markedly unequal in size. Abnormal specimens of the pygidium of *C. insolitus* n.gen., n.sp. form some 15 per cent of the total known, as compared to one injured free cheek of *D. scitulus* n.sp. in 38 specimens.

Ontogeny

It has been shown elsewhere (Whittington, 1956a) that the supposed odontopleurid protaspis described by Beecher is a phacopid. Whittington and Evitt (1954, pp. 28-31) described the meraspis and later ontogeny of two species of *Ceratocephala*, and made general observations on odontopleurid ontogeny. This section supplements the earlier account. Here odontopleurid protaspides are described for the first time, the three best-known examples (Pl. 3, figs. 1, 2; Pl. 4, figs. 1-5; Pl. 6, figs. 1-5; Text-figs. 9, 11) being different species of *Diacanthaspis*. Most remarkable is the presence of fixigenal spines. The spines on the dorsal surface are relatively large and arranged in a symmetri-

cal pattern (numbered and lettered here as in Text-fig. 1), there being a median occipital, three pairs on the glabella (2-4), and a pair on the anterior border just in front of 4 and slightly farther apart. On the glabella the occipital furrow is shallow, and in *D. cooperi* and *D. lepidus* n.sp. the basal glabellar lobe is faintly delineated. The eye lobe is situated near the antero-lateral border of the cheek, the two branches of the suture aligned and isolating a narrow (tr.) free cheek, which bears a row of border spines, the posterior the longer. The posterior branch of the suture cuts the margin immediately outside the fixigenal spine. A rostrum is present and the hypostome relatively large. The succeeding Stage 0 of each of these three metaprotaspides is known (Text-figs. 9C, 11B; Pl. 4, fig. 6) as is Stage 0 of *Apianurus barbatus* n.gen., n.sp. (Text-fig. 22A). Fixigenal spines persist, but long, stout librigenal spines are also present in species of both genera. Some additional spines (including axial 5 in *A. barbatus*) appear on the dorsal surface.

In the next largest specimens known of *Diacanthaspis* (Text-figs. 9D, 11C) and *Apianurus* (Text-fig. 22B), specimens which must represent the exoskeleton at Stage 1, the stout fixigenal spine has disappeared. There is no trace of where it has been, unless it is represented in *Apianurus*, greatly reduced, by one of the tiny spines between B and C on the extremity of the posterior border (Text-fig. 22B). However, there are tiny spines in this position in the smaller cranidia between B and the fixigenal (Text-fig. 22A), and most probably these are the spines seen at the extremity of the posterior border in the next stage. One or two specimens (Pl. 19, figs. 4, 6) of *Apianurus* have the fixigenal on one side and not on the other. It is hard to know whether this is the result of accidental breakage (and the fragility of the specimen at the base of the spine makes this likely), or whether it is showing the abrupt loss of the fixigenal on one side before the other. The course of the posterior branch of the suture is a curve across the ventral side of the base of the fixigenal spine. After the fixigenal is lost, the curve is similar, but runs across where the dorsal side of the base would have been. Thus little modification of the course of the posterior branch of the suture, and of free cheek outline, is caused by the loss.

In *Diacanthaspis*, spines A₁, B, C, D, and the fixigenal are

present on the postero-lateral part of the fixed cheek of the protaspis and Stage 0 cranidia. In the next largest size the fixigenal is gone and A₁, B, C, and D remain. The free cheek shows no sudden modification as the fixigenal is lost — the eye lobe moves back and the course of the sutural branch is altered slightly accordingly (Text-fig. 9D).

Thus the cephalon of *Diacanthaspis*, and of *Apianurus*, is, at about Stage 1, "opisthoparian." Evidently the change takes place rapidly, for there is little difference in size between cranidia with and without the fixigenal spine (e.g. Pl. 6, figs. 6, 8; Pl. 19, figs. 2, 4, 9). If the loss is by reduction, as it is in such genera as *Sphaerexochus* (Whittington and Evitt, 1954, Pls. 17 and 32) or *Elcricalymene* (Whittington, 1941, Pl. 72), then this reduction is a far less gradual process in odontopleurids. No transitional specimens showing such a gradual reduction have been found, however, and the evidence points to the process being one of abrupt loss taking place, perhaps between moults, in the transition from Stage 0 to Stage 1.

The Stage 0 exoskeletons of *Diacanthaspis* and *Apianurus*, genera placed in separate subfamilies, are so similar that we may reasonably expect other odontopleurid protaspides to be like those of *Diacanthaspis* — gently convex; fixigenal spine like the two on border of protopygidium; free cheek narrow (tr.), bearing a librigenal spine; eye lobe far forward on the antero-lateral slope; glabella parallel-sided, divided by the occipital furrow, in front of which there may be small, low, basal lobes, and bearing a median occipital and, if any axial spines, numbers 2, 3, 4, and perhaps 5; fixed cheeks bearing some or all of the spines lettered in Text-figure 1. The Stage 0 cranidium of *D. ulrichi* (Text-fig. 12A) shows how smooth the external surface may be, compared to that of *D. lepidus* or *D. secretus*.

The meraspid development of the different genera also proceeds along parallel lines — as has already been observed in species of *Cratocephala* and *Diacanthaspis* (Whittington and Evitt, 1954, pp. 28-31). In *Diacanthaspis cooperi* and *D. lepidus* n.sp., small, low, basal lateral glabellar lobes are present in the metaprotaspis at the base of the gently inflated fronto-median glabellar lobe, and the axial furrows are broad and shallow. The second lateral lobes appear later, after Stage 0. In *D. secretus*

the basal glabellar lobes are not apparent until after Stage 0, but this may be because they are obscured by the large spines on the external surface. In *Ceratocephala* the fronto-median glabellar lobe is strongly convex in the earliest known stages (Text-fig. 16), standing high above the broad axial furrows. At the next known stage (Pl. 14, fig. 2) basal glabellar lobes appear in the trough of the axial furrows. Thus, as pointed out previously (Whittington and Evitt, 1954, p. 29), the strongly convex axial region of the tiny *Ceratocephala* cranidium is homologous with the fronto-median lobe only of later stages, and the true boundaries of the glabella lie somewhere just outside, in the axial furrow. In the protaspis of *Diacanthaspis* the second segment (axial 2) is the longest (sag.), and axial 5 unmarked. In early meraspid stages of *Ceratocephala* (Whittington and Evitt, 1954, fig. 16; 2a is labelled "2"), *Apianurus* (Text-fig. 22B), and some species of *Diacanthaspis* (e.g. Text-fig. 9D), axial 2 is conspicuously longer and axial 2a is present. Axial 3 and 4 are progressively shorter, and 5 (which appears in *Apianurus* at Stage 0 but later in some species of *Diacanthaspis*), is the shortest. Subsequent growth of the glabella continues this trend, the second segment expanding and lengthening, the third likewise, but to a lesser extent, and the fourth and fifth remaining short. Neither 4 nor 5 disappears completely, and it seems unlikely that 4 disappears in *Leonaspis*, as implied by Hupé (1953, p. 102, fig. 62 (3)).

In the odontopleurid protaspis, as in those of, for example, cheirurids, phacopids, calymenids, and pliomerids, the eye lobe is situated inside the margin of the cheek, a short way up the antero-lateral slope. The facial suture is completely developed and is not marginal, and, in the late metaprotaspis (if not before), rostral, connective, and hypostomal sutures are present. The backward migration of the eye during ontogeny occurs in all odontopleurids, and is most marked in odontopleurinids and apianurinids.

A characteristic feature of odontopleurids is the way in which the antero-lateral extremity of the occipital ring merges into the inner corner of the cheek, and thus the posterior border is widest (exs.) distally, narrowing proximally to disappear at the axial furrow. At Stage 0 in *Diacanthaspis cooperi* (Text-fig.

9C), and in slightly later stages of other species of *Diacanthaspis* (Text-fig. 11C, 11D), in *Ceratocephala* (Text-fig. 16), and in *Apianurus* (Text-fig. 22C), there is a spine (Δ_1) in the inner corner of the free cheek where it passes into the occipital ring, and the posterior border widens (exs.) rapidly outwards. In later stages inflation of the inner corner of the fixed cheek accompanies the expansion of the posterior part of the glabella and backward movement of the eye lobe.

The border spines of the protopygidium and early transitory pygidium of *Diacanthaspis*, and of the early transitory pygidium of *Apianurus*, become respectively posterior pleural, and pleural, spines of the thorax. Anterior pleural spines are tiny and appear low down on the edge of later transitory pygidia of *Diacanthaspis* (Pl. 3, fig. 18), but never appear in *Apianurus*. The earliest known transitory pygidia of *Ceratocephala* (Whittington and Evitt, 1954, Pl. 8, fig. 4; Pl. 26, fig. 1) have the two types of border spines, those corresponding to the posterior pleural being relatively larger, as they are in the thorax.

Attention has been drawn to the likenesses between early developmental stages of different odontopleurid genera, i.e. to the generalized family characters appearing first in ontogeny. Although the later developmental stages follow a somewhat parallel course, it is also true that out of the general characters the more special characters are developed, so that during ontogeny each species diverges more and more from all others as it takes on its distinctive holaspid form. No better example of von Baer's "laws" could be wished for (cf. de Beer, 1951, pp. 2-3). At Stage 0 we can clearly recognize not only family but generic characters, and the ontogenies of the species of *Diacanthaspis* suggest that specific characters are recognizable at this stage, and probably still earlier, in the metaprotaspis. Thus, in the earliest known ontogenetic stages, while general characters are most obvious, special characters are expressed in the details of morphology. Could we go farther back in ontogeny, into the anaprotaspis stages and embryonic stages, we might find those points at which only higher systematic categories — superfamily, order, or even class — are recognizable.

Locus of Segmental Divisions

The occurrence of axial spine pairs, and of transverse, sym-

metrical spine-rows in the protaspides and Stage 0 specimens of odontopleurids is emphasized by the new evidence given here (Text-figs. 9, 11, 22), and is manifestly a fundamental character. On the cephalon (Text-fig. 1), spines A_1 , B, and C form a row with axial spines 1, A_2 and D with axial 2, A_3 with axial 3, Er and Pl with axial 5. These rows seem without much doubt to reflect segmentation, and the fixigenal spine, with B at its base, belongs to the posterior row. Each of the two or three border spines of the protopygidium has an upwardly-directed spine at its base (Pl. 3, figs. 1, 3; Pl. 4, figs. 1, 4; Pl. 6, figs. 1, 5, 10; Pl. 19, fig. 5), and the homology with the fixigenal and spine B is clear. These border spines of the protopygidium will become successive posterior pleural spines of the thorax. Thus there seems no reason to doubt that the joint between cephalon and protopygidium corresponds with a primary segmental division in the animal, as do the joints between successive thoracic segments, and that the fixigenal and posterior pleural spines are homologous.

The holaspid exoskeleton affords evidence in support of this interpretation, and three examples may be offered:—

1) *Primaspis ascitus* (Pl. 1, figs. 1, 11, 14). Posterior, most convex part of occipital ring, curving forward distally to occipital lobe, parallels structure and ornament of thoracic axial ring; posterior border is narrow (exs.) and smooth proximally, widened and inflated distally and tuberculate, as is the posterior band of the thoracic pleura; posterior border furrow is like pleural furrow; anterior band of pleura must correspond to most posterior part of cheek.

2) *Diacanthaspis ulrichi* n.sp. (Pl. 8, figs. 1, 12, 13, 21, 24) affords corresponding evidence, the spines on occipital and thoracic ring, and on posterior border and posterior band, being similar in size and arrangement.

3) *Calipernurus insolitus* n.gen., n.sp. (Pl. 23, figs. 3, 5, 7; Pl. 24, fig. 16). The highest, median part of the posterior border and lateral part of the occipital ring form a conspicuous smooth band, which seems to pass behind the paired occipital spines, and distally ends a short distance inside the suture. On the thoracic segment the smooth band runs along the highest part of the axial ring and pleural ridge.

Many other examples could be used, and it is notable that, in some, one could readily assume that the librigenal and posterior pleural spines were corresponding structures. This does not appear likely, however, in the apianurids, and early ontogenetic stages of odontopleurids seem to preclude this view and to show that the librigenal spine belongs to some segment in front of the occipital.

Study of the pygidium of *P. ascitus* n.sp. (Pl. 1, fig. 9) and of *D. ulrichi* n.sp. (Pl. 8, fig. 6) shows how like the posterior band and posterior pleural spine is the pleural ridge and major border spine. The Stage 8 transitory pygidium of *D. cooperi* (Pl. 3, figs. 17, 18) brings out strongly this likeness, and I have little doubt but that pleural ridge and major border spine of pygidium are homologous with posterior pleural band and spine. This means that the anterior 2 or 3 pairs of border spines are homologous with the anterior pleural spine, and their number is added to during ontogeny. For example, in *Apianurus barbatus* n.gen., n.sp., a small holaspid pygidium (Pl. 18, fig. 18) has one border spine in front of the ridge bearing the major spine, a larger holaspid has two (Pl. 18, fig. 12).

The similarity in structure between occipital ring, posterior border, and adjacent part of cheek and axial ring and pleura of thorax in odontopleurids has been noted before (Warburg, 1933). These trilobites afford no support for the view of Størmer (1942, p. 130) that "the transverse joint between the pleurae of the thoracic segments, or between these and the cephalon or pygidium, are secondary formations crossing the primary segments." Størmer based his argument mainly on an interpretation of *Holmia* and *Paradoxides*, and believed that in these trilobites each thoracic pleural spine belonged to the axial part of the segment in front of it (Størmer, 1942, text-figs. 14, 15a, 15e). In *Selenopeltis* (his text-fig. 15b) he represented the possible secondary segmentation as different in character, for each thoracic pleural spine belonged to the segment it was attached to, the "secondary segmentation" only affecting part of the pleura. There seems no evidence in odontopleurids for such a secondary joint, but in any genus other than *Selenopeltis*, which has the peculiar forward bend of the posterior pleural ridge, it would be hard to detect. Hupé (1953, pp. 118-119) does not support Størmer's suggestion.

Mode of Life

The spininess of the exoskeleton and the wide and seemingly rapid geographical distribution (many genera make their appearance almost simultaneously in two continents — Prantl and Přibyl, 1949, pp. 209-212) of many genera have led most students to regard odontopleurids as floating in habit (e.g. Prantl and Přibyl, 1949, pp. 132, 209; Whittington and Evitt, 1954, pp. 32-33, and references). The present study provides additional evidence for the view elsewhere expressed (Whittington, 1956b) that the convex cephalon will rest on a level surface on the anterior and lateral margins of the cephalon, the occipital ring the highest region, the posterior margin approximately vertical. In this position the thorax and pygidium, when stretched out horizontally, lie a short distance above the level surface. The outer surface of the hypostome lies roughly parallel to this surface and must be close to it. Antennular notches are commonly developed in the anterior cephalic margin, presumably so that the antennae may protrude forward while the animal rests on the cephalic margin. The cephalon is "propped" in this characteristic attitude by the development of either of two structures, or a combination of them. These are: (1) expansion of the lateral areas of the cheek, as in *Ceratocephala* (Whittington and Evitt, 1954, fig. 14), *Selenopeltis* and *Dicranurus* (Text-fig. 18); (2) development of a fringe of spines on the lateral cephalic border, increasing in length posteriorly, as in *Acidaspis*, *Dudleyaspis*, *Miraspis*, and *Diacanthaspis* (Text-figs. 10, 13-15). A combination of the two structures is seen in *Whittingtonia* (Text-fig. 17), and in *Apianurus* (Text-fig. 19) the basal parts of the librigenal spines act as "props." The possibility of resting in this position being universal among odontopleurids, and its attainment by the development of a variety of structures, attests that it was of fundamental importance, and that odontopleurids commonly rested in this attitude. It may well have been a feeding position on the sea bottom, movements of the appendages causing food-carrying currents to move forward under the head toward the mouth. This position — resting on the cephalic margins and with the thorax and pygidium stretched out above the bottom — is characteristic of diverse trilobites, such as Harpidae (Whittington, 1950, pp. 25-26), Bathyruridae (Whit-

tington, 1953, p. 651, Text-fig. 1), and some illaenids and cheirurids. It seems, therefore, that while the spinose exoskeleton probably aided the animal in floating, and may have had a protective function, other features point to the odontopleurid as having rested on the sea bottom for at least part of the time. We need not necessarily regard odontopleurids as entirely pelagic, then, but rather as drifting (and feebly swimming?) at some depth in shallow seas, and resting at times on the bottom. Odontopleurids occur in limestones ranging from light-coloured, coarsely crystalline to dark, aphanitic, muddy and silty, and in a variety of mudstones, shales, siltstones and fine sandstones. They seem to have been preserved in a wide variety of shallow water marine environments, and particular genera, and sometimes species, occur in a variety of rock types. This mode of occurrence might be used as an argument for their being mainly or wholly pelagic. The wide geographical distribution, however, does not necessarily imply a pelagic mode of life, for the early developmental stages were floating and would permit this wide distribution. It is notable that, in the development of *Diacanthaspis cooperi* (Text-fig. 9), the lateral cephalic spines develop rapidly in the earliest meraspid stages, after the fixigenal spines are lost. It may be at about this stage that the change from entirely floating to a partially bottom-dwelling mode of life occurs.

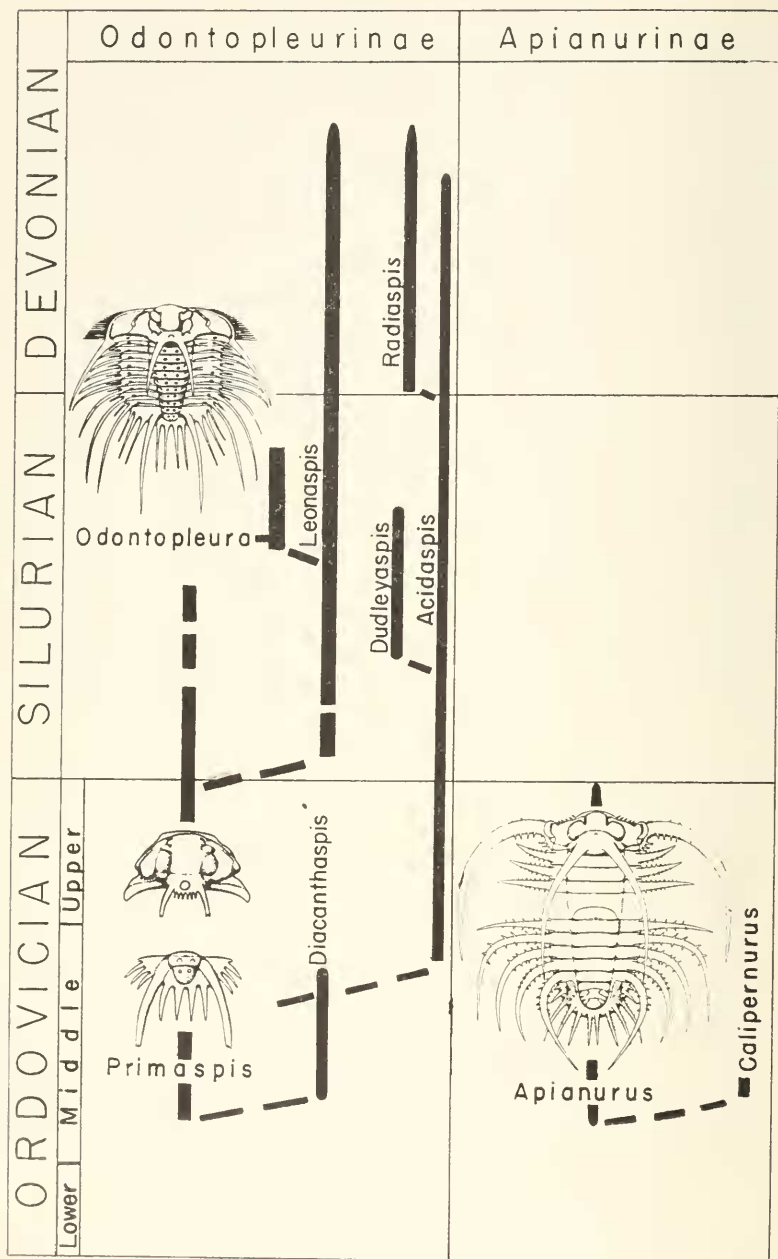
Origin and Evolution

Text-figure 3 summarizes my views on the taxonomy and evolution of the Odontopleuridae, and reasons for this arrangement are given in the systematic section. The earliest representatives of the family appear to be recorded from the Arenig (Canadian) — *Selenopeltis* in Shropshire, England (Whittard, 1952, p. 158), and pygidia of odontopleurinid type from Öland, Sweden (Bohlin, 1949, pp. 539, 560, 566). A pygidium of the latter type was described by Öpik (1926) as *Acidaspis solis*, and came from beds of early Llanviru age in Estonia. The cranidium described by Hintze (1953, Pl. 19, fig. 16) is of about the same age — late Canadian or immediately post-Canadian, and by this time *Selenopeltis* is widespread in western Europe and North Africa. By late Llandeilo time other genera have appeared — *Primaspis*

in Bohemia and *Ceratocephala* and *Apianurus* n.gen. in the Lincolnshire limestone of Virginia. Thus in a relatively short span of time odontopleurids appeared and diversified into the types here regarded as constituting four subfamilies. These early genera are at present known from widely separated geographical areas, and correlation between the rocks containing them, and thus relative times of appearance, can be only generalized. Thus one cannot with any confidence single out the earliest stock or a geographical area in which odontopleurids arose and from whence they spread out. Prantl and Přibyl (1949, p. 212) pointed to the Upper Ordovician of Scotland as the time and region where the first differentiation of odontopleurids took place, but this evidently is not so. Comparative morphology seems to throw no light on origins either, for other Canadian trilobites seem not to be closely related. The peculiarities of the odontopleurid protaspis serve to emphasize the lack of obvious relationship between the family and its contemporaries. In seeking the ancestors of the Odontopleuridae, "The possibility that groups hitherto soft-shelled were acquiring the power to mineralize the exoskeleton cannot be overlooked" (Whittington, 1954, p. 198; cf. Rasetti, 1948, p. 5). Yet as Professor R. Kozłowski has pointed out to me (personal communication), the sudden appearance of new types is a frequent phenomenon in the history of this and other animal groups, and alternative explanations can be offered for these appearances.

The initial diversification of the odontopleurids established the four subfamily types, illustrated in Text-figure 3 by *Primaspis*, *Ceratocephala*, *Apianurus* n.gen., and *Selenopeltis*. Though these

Figure 3. Classification, relationships and range in time of the genera of the Odontopleuridae. Characteristic members of each subfamily are shown, reproduced from Figures 4, 5, 19A, and 25C. *Ceratocephala* from Whittington and Evitt, 1954, figure 13. Range of each genus shown by solid black bar, bar broken if range uncertain. Broken diagonal lines suggest relationships between genera. Numbers of genera through time proportional to width of bar at right. Lower, Middle, and Upper divisions of the Ordovician correspond with the three Ordovician Series of Twenhofel et al., 1954.



Miraspininae		Selenopeltinae	Number of Genera
Miraspinis	Ceratonurus Dicranurus Koněprusia Selenopeltoides Orphanaspis		
	Ceratocephala		
	Proceratocephala C.(Ceratocephalino) Whittingtonia	Selenopeltis	

Figure 3

four groups have much in common, each has its distinctive characters, one of the most important being the type of hypostome (Text-fig. 2). There is no comparable diversification after this, for only two subfamilies survive the Ordovician and no new ones arise. In later Middle Ordovician times three (and possibly a fourth) new genera and one new subgenus arise (making a total of at least eight in the Middle Ordovician), and two new ones appear in Upper Ordovician times. During the Silurian period five new genera arise, and in the Devonian four. In the Middle and earliest Upper Devonian the nine surviving genera become extinct, this extinction being almost as rapid as the early diversification. Text-figure 3 shows the variation in time of number of genera and reflects the abrupt appearance and extinction of the group, though not the maximum morphological diversity of Ordovician time. A striking feature of odontopleurid evolution is the long range in time of certain genera—*Ceratocephala* endures for some 100 million years, and each of four other genera, *Primaspis*, *Leonaspis*, *Acidaspis* and *Miraspis*, for some 50-70 million years (on present estimates of absolute time). Other genera appear to have a relatively much shorter range. It is suggested here (Text-fig. 3) that certain of these long-ranging genera provided a root-stock from which the short-ranging genera were derived. *Ceratocephala* affords the best example, the other miraspid genera differing from it in one or more morphological characters (e.g. the big paired occipital spines of *Dicranurus*, or the inflated median glabellar lobe of *Whittingtonia*) but retaining the main structural plan. Not all the seemingly derived genera are short-ranging, e.g. *Miraspis*, though this genus may prove to be rather a closely related but distinct root-stock. *Acidaspis* and *Primaspis-Leonaspis* seem to be the root-stocks of the Odontopleurinae. The other two subfamilies are relatively short-lived, not so diverse, and the Selenopeltinae especially seem an aberrant off-shoot.

If any general picture is afforded by the pattern of odontopleurid evolution, it seems to be one of persistent main themes and relatively brief appearances of variations on these themes. Some of these variations, such as large, paired or single, occipital spines, major pygidial spines, marked inflation of certain glabellar lobes, appear more than once during the history of the family, and in different combinations, suggesting a process of shuffling

of morphological characters.

The stratigraphical position of each of the species of *Diacanthaspis* is shown in Text-figure 8. There appear to be three main strands within the evolving plexus of species, viz. *orandensis-cooperi*, *lepidus-secretus-scitulus*, and *ulrichi*-aff. *ulrichi*. The species are similar to each other, the distinctions being size and length of median and/or paired occipital spines, outline of glabella and degree of inflation of lobes, presence or absence of, and position of origin of, major pygidial spine, size and distribution of spines on external surface, etc. The illustrations show that these characters are relatively minor distinctions within a major framework, and that they appear and disappear, forming different combinations. Thus the species of *Diacanthaspis* show the same evolutionary pattern in a part of the family as in the whole—the presence of several main themes, occurrence of minor variations on these themes,* and shuffling and recombinations of characters within the plexus. No other genus is represented in the collections by as many species as is *Diacanthaspis*. In other genera represented by more than one species no particular trends of morphological change are evident.

Turning to consider the rate of morphological change among the silicified trilobites, it is seen to be variable in different lines during lower Edinburg to Oranda time—*Apianurus barbatus* n.gen., n.sp., shows no change, and there is little in the *Diacanthaspis ulrichi*—aff. *ulrichi* line, while the *D. lepidus-secretus-scitulus* line shows considerably more. *Ceratocephala* is present in the pre-Edinburg Lincolnshire limestone (*C. triacanthos* Whittington and Evitt, 1954), a second species *C. laciniata* is common in the lower Edinburg, and *C. rarispina* n.sp. is rare in the Oranda. Thus there is change in this presumed line of descent, though no particular trend is evinced. An apparent off-shoot from this line in the lower Edinburg is *C. (Ceratocephalina) tridens* n.subgen., n.sp. In Oranda to lower Martinsburg time there is slight morphological change in the *Diacanthaspis orandensis-cooperi* line.

The ontogeny of certain fossil animals has been interpreted as showing recapitulation of ancestral adult morphology, but no examples of this process have been adduced from trilobites. Following Stubblefield's suggestion (1936), Størmer (1942),

and most vigorously Hupé (1954), have urged that paedogenesis or neotony is an important process in the evolution of trilobites. In the case of *Diacanthaspis* we know the development in detail of the oldest and youngest species (Text-figs. 9, 11; Whittington, 1941, text-figs. 2-6), and something of that of other species (Text-fig. 12). However, not more than one complete ontogenetic series is known from any one of the three lines of descent in *Diacanthaspis*. Thus we do not have sufficient evidence to reveal whether or not recapitulation or paedogenesis are important processes in the evolution, but there are no indications of either being operative. What is clear is that the earliest developmental stages of the various species are remarkably similar, though even at this stage specific differences may be observed. As development proceeds through the meraspid stages the peculiar specific characters of each (long, paired, occipital spines, stout, median, occipital spine, shape of eye lobe, glabellar lobation, etc.) become increasingly evident. Thus the development of species of *Diacanthaspis* affords an excellent example of von Baer's laws (De Beer, 1951, p. 3). Comparison of the ontogeny of *Diacanthaspis* with that of *Apianurus* (Text-fig. 22) and of *Ceratocephala* (Text-fig. 16; Whittington and Evitt, 1954, text-fig. 16) shows that the early meraspid stages are remarkably alike, though generic and subfamily differences are quite evident. As development proceeds the divergence between genera increases. The protaspides of the Middle Ordovician odontopleurids suggest that, if paedogenesis were an important evolutionary process, we might expect, for example, holaspid Devonian odontopleurids to bear fixigenal spines, or to have only basal lateral glabellar lobes, or extremely short, paired, occipital spines. These expectations are not fulfilled. A clearer understanding of the evolutionary processes may be possible when ontogenetic series of later Ordovician, Silurian, or Devonian odontopleurids are known, but present evidence seems not to favour recapitulation or paedogenesis, and seems to suggest that the importance of this latter process in the evolution of trilobites in general may have been overestimated by Hupé (1954) and others.

PART II: SYSTEMATIC DESCRIPTIONS

Family ODONTOPLEURIDAE BURMEISTER, 1843

Diagnosis: Cephalon convex, so that postero-medial region stands high above antero-lateral margin. Glabella with maximum width generally at occipital ring, sub-parallel sided or tapering forward, occipital ring may be elongated (sag.) and prominent, lateral lobes may be present, median and/or paired spines or tubercles characteristic; 2-3 pairs of lateral glabellar lobes. Cheek convex, inner posterior corner merges with antero-lateral corner of occipital ring; eye lobe prominent, situated centrally on cheek or inside and behind this point, eye ridge present, anterior branch suture runs forward and inward, posterior branch outward and backward to cross posterior margin, sutural ridges characteristic. Librigenal spine usually stout, broad base merging with postero-lateral borders; commonly row of shorter spines arising from outer edge of border of free cheek, progressively shorter anteriorly; antennular notch in border of free cheek adjacent to anterior branch of suture. Rostrum short (sag. and exs.) and wide (tr.). Hypostome of width greater than, or equal to, length, postero-lateral margins rounded, convex middle body, faint middle furrows running backward and slightly inward from depression at antero-lateral corner of middle body, lateral and posterior border of moderate and similar width, small anterior wing, no wing process, posterior wing extremely small.

Thorax of 8-10 segments, convex axial ring and long articulating half-ring; pleura horizontal, gently or moderately convex, undivided or divided into two bands, long pleural spine on posterior band, directed outward and progressively more strongly backward posteriorly, short pleural spine or spines on anterior band, directed outward and downward. Either or both pleural spines may be missing from the first (and sometimes second) segment because of the size of the facet. Pygidium short, sub-triangular in outline, 2 axial rings, may be faint third ring; row of horizontal border spines, one pair often larger than remainder, may be upwardly directed, and with base connected by low pleural ridge across pleural region to first axial ring; or major spine may arise from pleural region.

External surface of exoskeleton rarely smooth, generally with

thorn-like spines or tubercles, granules between them, arrangement of larger spines or tubercles may be symmetrical about midline. Scattered openings occur near tips of large spines (librigenal, posterior pleural, major pygidial), and sometimes also at tips of thorn-like spines or tubercles. Latter may, however, be closed at tip, or may exhibit several tiny openings. Four tiny depressions, arranged at corners of square, may occur at summit of median occipital tubercle.

Doublure narrow, curled under. Appendifers not developed.

Geological Range: Late Lower Ordovician (late Canadian or Arenig) to early Upper Devonian.

Discussion of Systematics of Odontopleuridae

Since Prantl and Příbyl published (1949) their new arrangement of the Odontopleuridae, it has been followed, with some emendation, by Erben (1952a, 1952b), and adopted with reservations by Hupé (1953). Whittington and Evitt (1954, pp. 52-53) voiced some criticisms, and these and others are explained in detail here. Study of the silicified material, and of type specimens of most genera (Whittington, 1956b), has provided a wealth of new data, and my taxonomic scheme is summarized in Text-fig. 3. This adds a new group, but retains the three main groups of Prantl and Příbyl, assigning to them subfamily rather than family rank. I consider the homogeneity of the odontopleurids, as well as the relatively small size of the group, suggestive rather of family than superfamily rank (cf. Hupé, 1953, p. 230). The similarity of early larval stages of different genera may be interpreted as indicating a monophyletic origin for the family and not "at least diphyletic" as maintained by Prantl and Příbyl (1949, p. 131). In subdividing odontopleurids those authors laid emphasis on the form of the cephalon, and particularly the hypostome, the "different origin of the genal spines," and the direction of the posterior pleural thoracic spines. With some of these I agree, while others seem unimportant. I have based the subfamilies here used principally on the following:—

a) Form of the hypostomes, which, while all are of a type peculiar to the family, seem to fall into four sub-types corresponding with the subfamilies (Text-fig. 2).

b) Form and inflation of the glabellar lobes and occipital ring. The characters of this region are of prime importance in sub-

family divisions, and their nature is summarized in the diagnoses.

c) Form of the cheek and position of eye lobe, which together help to determine the course of the dorsal facial suture and the angle between the two branches.

Such features as type of occipital spine or spines, form of thoracic segments, direction of posterior pleural spines, shape of pygidium and development of major border spines seem to me to be of less importance. Whittington and Evitt (1954, p. 32) suggested that the librigenal spine of *Ceratocephala* did not arise in a fundamentally different way from that of *Diacanthaspis*, and further evidence for this view is given here. Thus I do not accept the suggestion that a major systematic division may be based on the supposedly different origin of this spine in different genera (Prantl and Přibyl, 1949, p. 131).

A forward direction of the posterior pleural spines of the first two or three thoracic segments is observed in some miraspid and in apianurid genera. In these forms the librigenal spines are well outside the distal parts of the anterior thoracic segments, and so this direction of the pleural spines is possible. In odontopleurid genera the librigenal spine is sometimes broad-based, and is directed back just outside the distal parts of the anterior thoracic segments. Hence these segments are faceted, and may lack pleural spines, or they are short. This difference in direction of the pleural spines of the anterior thoracic segments was regarded as important taxonomically by Prantl and Přibyl, but it is really dependent on the form of the cephalon, and in my view of little taxonomic value (cf. Whittington and Evitt, 1954, p. 52).

Subfamily ODONTOPLEURINAE BURMEISTER, 1843
(=Odontopleuridae of Prantl and Přibyl, 1949)

Diagnosis: Greatest width of glabella at occipital ring, tapering forward slightly or moderately: occipital ring may be elongated, median or paired tubercles or spines. Eye lobe far back, variable distance out across cheek, angle between two branches of suture near eye lobe 90-120°. Librigenal spine slim to stout, row of border spines on cheek well-developed. Hypostome (when known) slightly wider than long, middle furrow commences in front of mid-length and runs inward at a low angle; shoulder sharp. Lateral notch shallow. Pleurae of thorax

with broad (exs.), convex, posterior band, continuous with stout posterior pleural spine. Pygidium usually with major pair of border spines, 1-2 pairs small border spines between them.

Geological Range: Middle Ordovician to early Upper Devonian.

Discussion: Prantl and Přibyl (1949, pp. 135, 151, etc.) divided this group into two parts, the first (their *Odontopleurinae*) including *Odontopleura*, *Acidaspis*, *Primaspis*, *Radiaspis* and *Diacanthaspis*. In this group the anterior branch of the facial suture is said to run just outside the eye ridge, so that no subtriangular area is enclosed between suture, eye ridge and the anterior cephalic margin. In the second group (their *Acanthalominae*) which included *Leonaspis* and *Dudleyaspis*, a striking subtriangular area was claimed to be developed. Text-figures 4, 5, 7, 10, 13, 14 suggest that such an area is variously developed in all these genera, and that it scarcely affords a basis for a subfamily division. An additional distinction between the two groups was the "configuration of the occipital ring and the origin of the occipital spines" (Prantl and Přibyl, 1949, p. 135). I do not regard such differences as of this high a value. An example of our different points of view is our treatment of *Dudleyaspis*. Prantl and Přibyl (1949, pp. 171-172) regarded this genus as allied to *Leonaspis* because of the presence of the subtriangular area enclosed between the anterior branch of the suture and the eye ridge. This area seems to me to be no larger than that in *Acidaspis*, and the glabella lobation and cephalic form of these two genera are extremely similar, and I therefore regard them as allied, and *Dudleyaspis* as derived from *Acidaspis*.

Genus ODONTOPLEURA Emmrich, 1839

Text-figure 4.

Type Species: *Odontopleura ovata* Emmrich, 1839 (= *O. prœvosti* Barrande, 1846). See Prantl and Přibyl, 1949, p. 135.

Discussion: Only the type and one very similar species, from the Wenlockian of Europe, are known. *Odontopleura* is distinguished from *Leonaspis* (Text-fig. 7) by the larger, more elevated, lateral glabellar lobes (particularly the basal pair), the elevation and elongation of the median part of the occipital ring, which bears paired spines, the faintly defined occipital lobes,

the smaller eye lobes, situated farther outward and forward, and consequent different direction of the anterior branch of the suture, the slim librigenal spine and more numerous lateral border spines, the long anterior pleural spine and slimmer, less backwardly directed posterior pleural spine of the thorax, and the relatively wider (tr.) pygidium.

In glabellar lobation, convexity of cheeks, position of eye lobes, course of facial sutures, etc. *Odontopleura* approaches

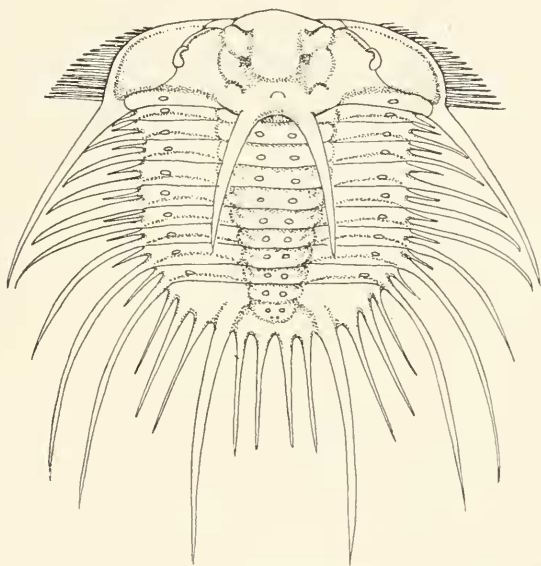


Figure 4. *Odontopleura ovata* Emmrich, Middle Silurian, Motol Beds, ea₂, Bohemia. Reconstruction, dorsal view, X 11 $\frac{1}{3}$. Based on MCZ 4170, Butovice; MCZ 4164, Lodenice.

Primaspis (Text-fig. 5), but is distinguished by the form of the occipital ring and stouter occipital spines.

Prantl and Přibyl (1949) reproduced some of Barrande's drawings and also new photographs, but all these illustrations are of specimens flattened in shale, as is that of Hupé (1953, fig. 134). In my drawing I have endeavoured to portray the convex cephalon in its true relation to the thorax, using uncompressed specimens from Butovice, Bohemia.

Genus PRIMASPIS R. and E. Richter, 1917

Text-figure 5.

Type Species: *Odontopleura primordialis* Barrande, 1846. See Prantl and Přibyl, 1949, p. 144.

Diagnosis: Glabella with small third lateral lobes, greatest width across occipital ring and basal lobes, occipital ring not

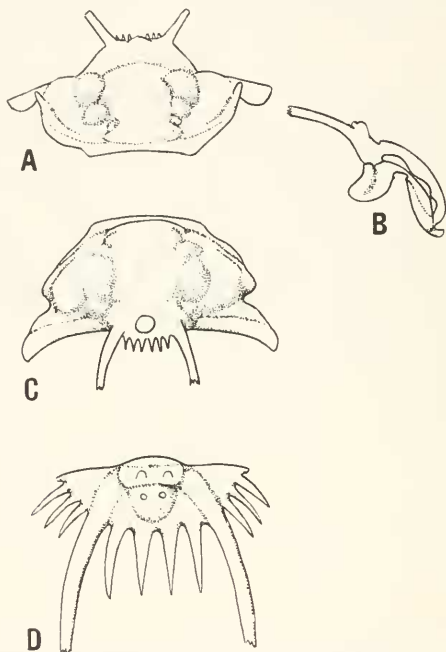


Figure 5. *Primaspis primordialis* (Barrande), Middle Ordovician, Drabov quartzites, dō, Bohemia. A, B, C, cranidium, anterior, right lateral, and dorsal views respectively, X 3. D, pygidium, dorsal view, X 3. Based on MCZ 4139, Drabov.

greatly inflated or lengthened, bearing median tubercle or paired spines, small occipital lobes. Eye lobe far back and at about half width of cheek. Lateral border spines short, librigenal spine broad at base. Thorax of ten segments, posterior pleural band inflated at fulcrum and continued into stout posterior pleural spine: anterior pleural spine small.

Discussion: This genus is represented in Bohemia by species ranging in age from Upper Llandeilo to Ashgill, and perhaps Silurian. *Primaspis keyserlingi* (Barrande, 1846) shows the characteristic features of the genus including the anterior pleural spines, which are not lacking (as stated by Prantl and Přibyl, 1949, p. 14), but is unusual in that the lateral glabellar lobes are fused, there are no occipital spines, and the external surface is smooth. In North America, *Primaspis* is represented by *P. ascitus* n.sp. (described below), *P. trentonensis* (Hall, 1847) (Whittington, 1941, p. 502, Pl. 74, figs. 31-37; Prantl and Přibyl, 1949, p. 149), and probably by *P. crosotus* (Locke, 1843) from the Eden of the Cincinnati district. All these species have a median occipital tubercle, but not paired spines. In the size and convexity of the basal and median lateral glabellar lobes, position of the eye lobe, course of the facial sutures, form of the pygidium, etc., such species as *P. crosotus* approach typical *Leonaspis*, and Prantl and Přibyl (1949, p. 146) have remarked on the *Primaspis* features displayed by *Leonaspis coronata* and *L. deflexa*. This seems to me to point to the derivation of *Leonaspis* from *Primaspis*, as suggested in Text-figure 3. The close relation of *Odontopleura* to these genera has been discussed.

Text-figure 3 also suggests that *Acidaspis* (Text-fig. 13; Whittington, 1956b) is related to *Primaspis*. Such a species as *P. trentonensis*, for example, has a strikingly similar thorax and pygidium, with the posterior pleural bands inflated at the fulcrum, and while the cephalon does not display the special features of *Acidaspis*, it resembles it in having the median lateral glabellar lobe considerably smaller than the basal, in convexity of cheeks, position of eye lobe, course of facial sutures, etc.

PRIMASPIIS ASCITUS Whittington, n.sp.

Plates 1 and 2; Text-figure 6

Holotype: USNM 116515 (Plate 1, figures 1, 2, 5, 6); locality 10.

Other Material: Paratypes USNM 116516a-h; all figured specimens in USNM.

Geological Horizon and Locality: Lower Martinsburg shale, locality 10.

Description: Cephalon crescentic in outline, moderately convex

longitudinally, strongly convex transversely. Glabella widest across basal lobes, slightly narrower at occipital ring, narrowing rapidly anteriorly, where it overhangs the border slightly. Occipital ring longest (sag.) medially, where it slopes gently forward to shallow occipital furrow; laterally, behind basal glabellar lobe, a low occipital lobe is developed, defined most clearly on the inner side by a shallow depression. Low median occipital tubercle. Occipital furrow deeper laterally. Three pairs of lateral glabellar lobes, basal (first) largest, sub-oval in outline, inflated and standing above part of median lobe separating them; second lobes inflated, defined by basal and second furrows directed inward and backward at about 45° , the basal furrow deepest at the inner end; inner ends of second and basal furrows joined to each other and to occipital furrow by shallow longitudinal furrow; anterior (third) lateral lobes with faint independent convexity, defined by a short, shallow furrow running inward from the antero-lateral corner of glabella. Axial furrows faint beside glabella, where fixed cheek merges with antero-lateral corner of occipital ring, clearly defined beside lateral lobes, dying out anteriorly where eye ridge merges with glabella. Narrow anterior border separated from glabella by shallow furrow. Cheek most strongly convex in inner corner inside eye lobe, which is situated at about half width (tr.) and close to posterior margin, opposite posterior portion of basal glabellar lobe. Palpebral lobe short, low, defined on inner side by deep palpebral furrow which curves around behind eye lobe and dies out. Anteriorly palpebral lobe and furrow merge with broad eye ridge and furrow on inner side. Eye surface with facets faintly discernible on inner side (Pl. 2, fig. 22). Anterior branch of suture runs forward and then curves inward a short distance outside eye ridge, crosses border furrow on low sutural ridge and meets rostral suture at edge of border. Posterior branch runs in "S" curve back from eye lobe, out across cheek, crosses border furrow on sutural ridge, and runs over border to doublure beneath base of librigenal spine. Anterolateral border of cheek moderately convex, margin curves forward just outside anterior branch of suture. Row of short border spines, increasing in length posteriorly, directed down and slightly out from lower surface of border. Posterior border narrow (exs.) beside occip-

ital ring, widening and swelling outward to merge with the broad base of the librigenal spine. Doublure of cephalon of same width as border. Low projections formed by inwardly projecting outer part of occipital furrow and the three glabellar furrows, particularly the deeper, inner part of the basal furrow. Small depression, with sharply raised anterior edge, in doublure in front of librigenal spine (Pl. 1, fig. 4), is the socket for fulcral process of anterior segment of thorax. Rostrum unknown, but evidently a transverse plate on outer edge of anterior border, perhaps curled under at hypostomal edge. Hypostome slightly wider than long, gently convex middle body, middle furrow running backward and inward a short distance from circular depression at antero-lateral corner, macula faintly defined by convexity, tips of crescentic posterior lobe slightly inflated. Narrow anterior border not defined by furrow; lateral border with small, triangular anterior wing directed dorsally, small lateral notch and sharp, swollen shoulder projecting outward; postero-lateral border widest, gently convex, small median projection in faint, wide median notch. Doublure extending between shoulders, of same width as borders, posterior wing a small, twisted projection (Pl. 1, fig. 18), inner edge of doublure curled in in medial portion. External surface of exoskeleton tuberculate, except in deeper parts of furrows, anterior border (which is granulate), inner part of posterior border, median area of posterior lobe of middle body of hypostome and adjacent maculae, and doublure (except median part of hypostomal doublure). Tubercles vary in size, larger ones may display symmetrical arrangement, including 5 or 6 pairs on fronto-median lobe, some on lateral lobes, and fixed cheek inside eye lobe. Toward tip of genal spine (Pl. 2, fig. 10) tubercles become longer and distally directed, and there appear to be tiny openings at the base on the distal side of some of them. Other tubercles closed at top. Median occipital tubercle with 4 tiny depressions (not the openings of canals through the exoskeleton) arranged in a square, and sometimes a small central pit (Pl. 2, figs. 21, 23).

Number of thoracic segments unknown. Convex axial ring narrowest in mid-line, where it slopes gently forward to deep articulating furrow. Latter with steep anterior slope, articulating half-ring long (sag.). Horizontal pleurae divided by slightly

diagonal pleural furrow into gently convex anterior band and strongly convex posterior band. Anterior pleural spine blade-like, shorter on anterior segments, facet at antero-lateral corner of segment. Posterior pleural band becomes more swollen distally at fulcrum, and is extended into spine, which is short on anterior segments, progressively longer and more backwardly directed on succeeding segments. Ring process and socket well developed, but axial socket and process inconspicuous. Anterior surface of pleura is flattened, with a projecting rim along the upper edge, and this surface fits against the flattened surface of the posterior flange, the projecting rim fitting against and above the curved upper edge of the posterior flange (Pl. 1, figs. 12, 13). Doublure extends in to fulcrum, and has an anterior projection, the fulcral process, which fits into the notch (with raised anterior edge to act as a "stop") in posterior part of doublure (Pl. 1, fig. 15). Axis of pygidium with strongly convex first ring, articulating furrow and half-ring as in thorax, second axial ring lower and less convex, tip of axis merging into border. Pleural regions flat, bounded by a low border anteriorly, strongest antero-laterally, and a broader, more convex postero-lateral border; crossed by a strong ridge connecting first axial ring to the base of major border spine. Five smaller spines, longest posteriorly, project horizontally from postero-lateral border and one major spine (with a swollen base which merges with proximal part of fourth horizontal spine) arises from upper, outer part of posterior border and projects upward and backward. Doublure curled under, as wide as border, at tip of axis most strongly curled and with a slight inward projection, inner, anterior corner forming fulcral articulating process. External surface of thorax and pygidium tuberculate, tubercles densely packed on axial rings, posterior pleural spines and pygidial border spines, less closely packed in articulating furrow and on pleurae and pleural regions, and absent from upper surface of posterior pleural band, articulating half ring, and inner part of doublure. On under side of proximal parts of spines tubercles smaller. Conspicuously larger tubercles as pair on posterior slope of axial ring, including two rings of pygidium, and a third pair (or row of 3) close together at the tip, suggesting a third segment. Large tubercles also in row along anterior pleural band, and one at

about half width (tr.) of posterior band, on posterior slope. Towards tips of thoracic posterior pleural and pygidial border spines tubercles elongated and distally directed, and some openings occur at bases of these tubercles. Elsewhere tubercles closed, and particularly the larger ones appear to expand slightly distally to give a bulbous tip.

Discussion: *Primaspis ascitus* n.sp. is extremely similar to *P. trentonensis* (Hall; see Whittington, 1941, pp. 501-502, Pl. 74, figs. 31-37) from the Trenton, Sherman Fall formation, of New York and Ontario. It differs from *P. trentonensis* in various minor ways, of which the more obvious are: 1) the greater convexity of the posterior part of the cephalon, so that the posterior surface of the basal glabellar lobes and fixed cheeks, particularly, is longer and descends vertically; 2) the inflation at the fulcrum of the posterior pleural band of the thorax is less; 3) the major border spines of the pygidium of *P. trentonensis* are farther apart, and the base does not merge with the distal part of the minor border spine inside it, but is separate. Also in *P. trentonensis* there are two minor border spines in front of the major spine, not three. Tubercles on the external surface are similarly developed and distributed in the two species, and the median occipital tubercle of *P. trentonensis* exhibits the four tiny depressions. Paired tubercles can scarcely be distinguished on the axis of *P. trentonensis*, except on the posterior edge of the two pygidial axial rings.

Development: Smallest cranidium of length (sag.) 0.6 mm. Text-figure 6A (cf. Pl. 2, figs. 1, 2) summarizes the characters: glabella narrow (tr.), almost parallel sided, basal lobes outlined, faint second lateral glabellar furrows, median occipital tubercle, large median tubercle (with a suggestion of a subdivision indicating that it will later divide and form axial spines 2a) opposite basal glabellar lobes, 3 distinct pairs of tubercles in front (axial spines 2-4); palpebral lobes about opposite axial spines 3, strong eye ridge running forward to antero-lateral corner of glabella, posterior border well-defined, widening (exs.) outward; tubercles on fixed cheeks and border in sub-symmetrical arrangement, including A₁, B, and C. Next largest cephalon known (Text-fig. 6B; Pl. 2, figs. 5, 6), length (sag.) 0.85 mm., shows considerable change. Both the cephalon as a whole, and individual parts,

are more convex. Fronto-median glabellar lobe now steep-sided, standing highest, basal and median lateral lobes well defined and inflated, width of glabella across basal lobes now 35 per cent width of cranidium, rather than 22 per cent as at the smaller stage. Eye lobe opposite anterior part of basal glabellar lobe, fixed

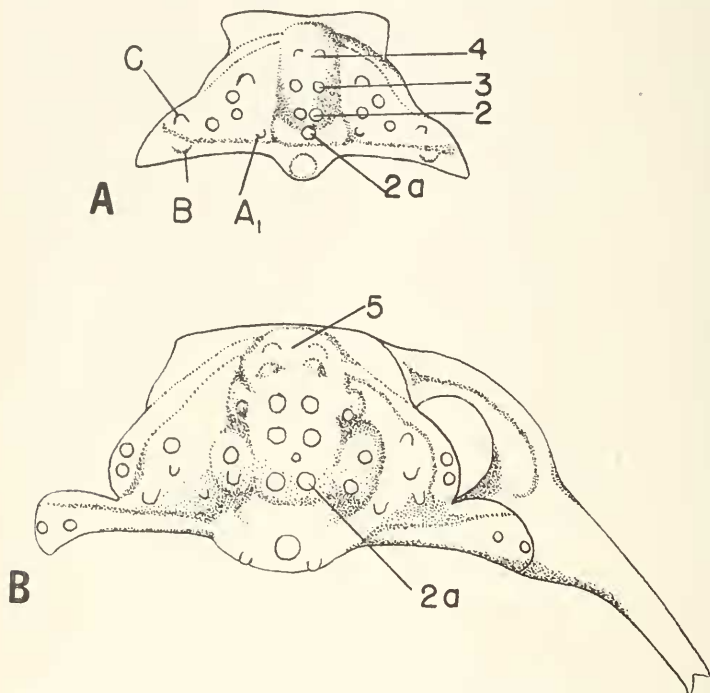


Figure 6. *Primaspis ascitus* n.sp. A, small cranidium, exterior view, drawn from original of Plate 2, figure 2. B, cranidium and right free cheek, exterior view, drawn from original of Plate 2, figure 6, and free cheek of appropriate size. X 38. Spines numbered and lettered as in Text-figure 1.

cheek inflated at inner corner, which merges with occipital ring. Median occipital tubercle large, low: on posterior margin of occipital ring prominent pair of tubercles, other pairs of smaller tubercles in front of these. Five pairs of tubercles on median glabellar lobe — axial 2a, 2-5 — the most anterior not quite sym-

metrical, paired tubercles on lateral lobes, larger tubercles on fixed cheeks and border sub-symmetrically situated. A larger cranidium of length (sag.) 1.2 mm. (Pl. 2, figs. 11, 12) shows that these trends of change have continued — convexity of lateral glabellar lobes and inner part of fixed cheek have increased, and fixed cheek and basal glabellar lobes are level with median glabellar lobe in transverse line. Width across basal lobes now 44 per cent width of cranidium. Eye lobe farther back, paired tubercles, including four on median glabellar lobe, may still be distinguished. In this size of cranidium, third lateral glabellar lobes and occipital lobes are distinct, as are 4 pits in median occipital tubercle. Further increase in size shows slight change continuing, so that width across basal glabellar lobes may become almost 50 per cent of that of cranidium; basal glabellar lobes are inflated sufficiently to stand above part of median lobe between them (Pl. 1, fig. 5); posterior slope of fixed cheek becomes steeper. The conspicuous larger tubercles of earlier stages lose their prominence and cannot be readily picked out in larger specimens. The smallest hypostome (Pl. 2, figs. 3, 4) differs little from larger ones.

Only transitory pygidium known (Pl. 2, fig. 9) is probably stage holaspid-1, since the portion behind the first segment is like the true pygidium, lacking only the first two lateral border spines. The axis is convex, each ring with a pair of prominent tubercles on the posterior edge — recalling the pair on the posterior margin of the occipital ring. Small true pygidia are like larger ones, but may have four border spines in front of the major spines, the anterior extremely short. In larger specimens this small anterior border spine is reduced, presumably with enlargement of the facet, and disappears.

Genus *LEONASPIS* R. and E. Richter, 1917

Text-figure 7.

R. and E. Richter (1952) regard as undesirable the revival of Conrad's (1840) name *Acanthaloma* by Prantl and Příbyl (1949, p. 151). I am in agreement with them, and have submitted a proposal for the suppression of this name to the International Commission on Zoological Nomenclature.

Type Species: *Odontopleura leonhardi* Barrande, 1846.

Diagnosis: Glabella as wide across large basal glabellar lobes as across occipital ring, two pairs glabellar lobes, the anterior

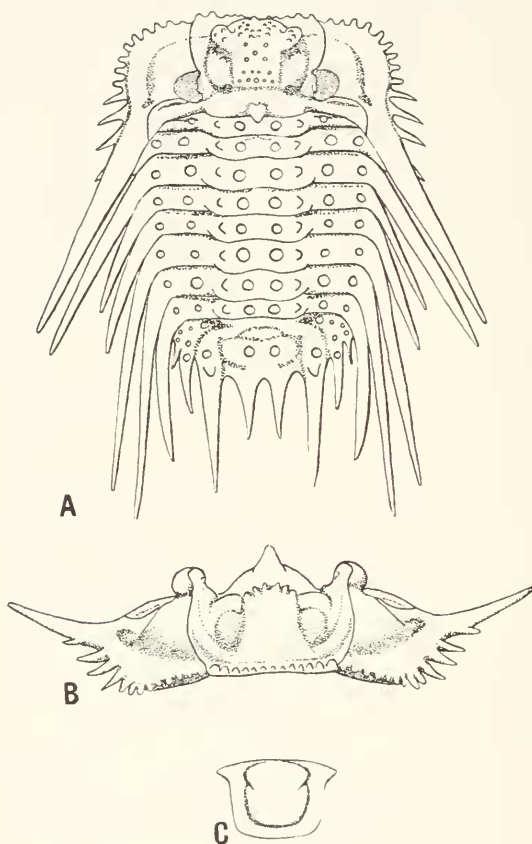


Figure 7. *Leonaspis* new species, Lower Devonian, Haragan shale, Arbuckle Mts., Oklahoma. A, complete exoskeleton, dorsal view. B, cephalon, anterior view. C, hypostome, exterior view. X 2. Drawn from originals of Whittington 1956b, Plate 57, figures 10-16.

smaller than the basal, occipital ring not greatly lengthened or inflated, median tubercle or short median spine. Eye lobe opposite posterior part of basal glabellar lobe or occipital furrow, large to medium size; two branches of suture almost at right angles adjacent to eye lobe, cross border furrows on sutural ridges. Librigenal spines broad-based. Thorax of 8-10 segments, pleurae with anterior pleural spines short, may be bifid distally, posterior band continuous with stout posterior pleural spine; anterior two or three segments may be faceted and pleural spines reduced. Pygidium usually with prominent pair major border spines, one or two pairs small border spines between them.

Geological Range: Lower Silurian to Middle Devonian.

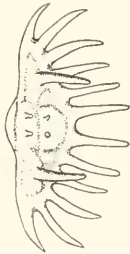
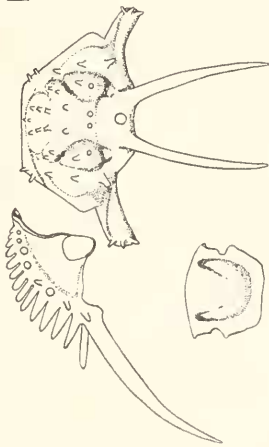
Discussion: Elsewhere (Whittington, 1956b) I have described two American species of *Leonaspis*, and one is illustrated here (Text-fig. 7). Both are very like the type species. I have also discussed the genus, and the unsatisfactory nature of the basis for the two subgenera of *Leonaspis* recently proposed by Prantl and Přibyl.

Genus *DIACANTHASPIS* Whittington, 1941

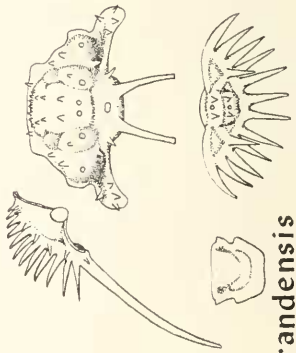
Type Species: *Diacanthaspis cooperi* Whittington, 1941.

Diagnosis: Glabella widest (tr.) across occipital ring and basal lobes, length (sag.) greater than maximum width; two pairs of lateral lobes, of which the anterior pair is the smaller, sometimes faint, tiny third lateral lobes; occipital ring with paired and median spines, of which one median and/or one pair may be conspicuously longer and thicker than the remainder; small lateral occipital lobes may be present. Eye lobe situated well inwards opposite basal glabellar lobe, sutural and eye ridges distinct. Row of spines on anterolateral cephalic border. Librigenal spine may be hooked at tip. Hypostome shield-shaped, width (tr.) across anterior wings and shoulders about equal; may be circular hole through doublure of shoulder. Number of thoracic segments unknown; pleurae with narrow anterior and broad posterior bands, latter not inflated at fulcrum. Pygidium

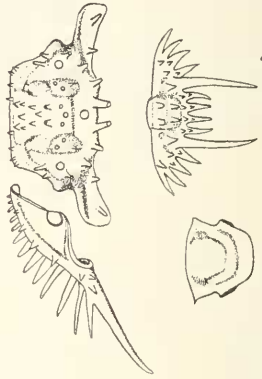
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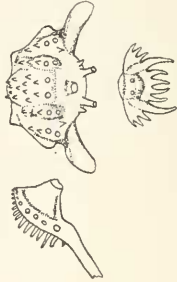
cooperi



orandensis



scitulus

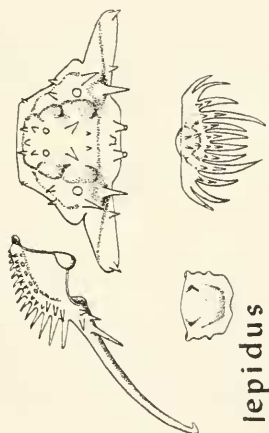


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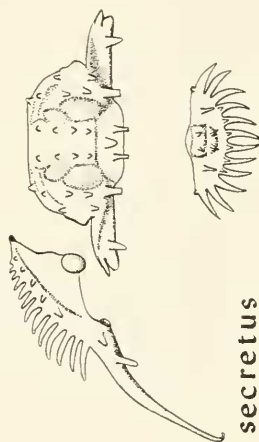
ORANDA FM

DIACANTHASPIS



ulrichi

lepidus



secretus

Figure 8. Comparison of species of *Diacanthaspis* in Middle Ordovician formations of Shenandoah Valley, Virginia. *D. lepidus*, *D. secretus*, and *D. ulrichi* are contemporaneous in the lower part of the Edinburg formation. Exterior views, main spines only shown on external surface. Approximately X 10.

of three segments, two axial rings distinct. Border with 6 or 7 pairs of horizontally directed spines, of which the 4th may be elongated; upwardly and backwardly directed major spine may be present on upper surface of border postero-laterally; major spines linked by ridge to first axial ring.

External surface of exoskeleton with median and symmetrically situated thorn-like spines on axial and pleural regions. granulation between these spines.

Geological Range: Middle Ordovician.

Discussion: The diagnosis has been emended to embrace the type and the new species shown in Text-figure 8. A recently described Scottish species (Tripp, 1954, pp. 663-664, Pl. 1, figs. 24-29) also lacks large paired occipital spines and major spines on the pygidial border, but appears to belong here. It also has faint third glabellar lobes, and such faint lobes are seen in *D. scitulus* n.sp. On the other hand, three Esthonian and Swedish species placed in this genus by Prantl and Přibyl (1949, p. 150) are here placed in *Apianurus* n.gen., and I consider it unlikely that "*Acidaspis*" *tremenda* Barrande, 1852, belongs in *Diacanthaspis*, as suggested by Prantl and Přibyl (1949, p. 150).

The similarities between *Diacanthaspis* and *Primaspis* have previously been commented on (Whittington, 1941, p. 502; Prantl and Přibyl, 1949, p. 150), and the similarities and contrasts are well illustrated by the Virginia species described here. The third glabellar lobes are clearly developed in *Primaspis*, and species of this genus have stout major pygidial spines. The inflation of the posterior pleural band at the fulcrum and of the outer part of the posterior cephalic border and base of the librigenal spine, are also characteristic of *Primaspis*, but not of *Diacanthaspis*.

The silicified species, though distinct from each other, have much in common, and they also fall into groups related in time — *lepidus* — *secretus* — *scitulus*, *orandensis* — *cooperi*, and *ulrichi* — aff. *ulrichi*, as discussed in Part I. These groups give a glimpse of the evolving plexus of *Diacanthaspis*, and might be regarded as subgenera, though this step is not taken here. The basic unity of all the species is shown by the similarity between the develop-

mental stages of each, a similarity which is most marked in the earliest stages. The basic unity is also shown by the presence of many common characters which are differently developed in different species, e.g. a relatively large median occipital spine is present in the tiny cranidia of *D. secretus* and *D. ulrichi*, but in the former it loses its prominence in later stages, while in *D. ulrichi* it is retained to the adult. The development of the paired occipital spines, present in all the young stages, offers another such example.

In all the species of *Diacanthaspis* there is a deep depression separating the basal glabellar lobe from the outer part of the occipital ring, the slope down to the depression from the occipital ring being gentle, that from the glabellar lobe steep. In *D. orandensis* and *D. cooperi* the forward-sloping antero-lateral part of the occipital ring develops a low, subcircular rise, bearing one or two thorn-like spines. This is the occipital lobe, a faintly developed feature peculiar to these two species.

The spines and granules on the external surface of the different species are described and illustrated in detail, and have been discussed in general terms in Part I. It should be emphasized that only in the best preserved specimens is the tip of the thorn-like spines seen to be truncated by a disk in which are tiny pits or openings. Their arrangement is not as regular as that of the four pits at the tip of the median occipital spine, and it seems unlikely that they are different-sized versions of the same structure.

DIACANTHASPIS COOPERI Whittington, 1941

Plate 3; Plate 9, fig. 6; Plate 11, figs. 16-18; Text-figures 8, 9.
Geological Horizon and Localities: Lower Martinsburg formation, localities 9-12.

Description: The new material enables the following additions to be made to the original description (Whittington, 1941, pp. 502-508, Pl. 74, figs. 1-30, text-figs. 2-6).

The eye surface is preserved in some specimens (Pl. 3, fig. 21; Pl. 11, fig. 17), the outer surface with the tiny facets faintly convex, corresponding pits on inner surface deeper. Librigenal spine ends in a sharp point, not a hook (Pl. 3, fig. 20).

Slightly larger hypostomes (Pl. 3, figs. 7, 9, 10, 13, 14) than those described previously have a length (sag.) little more than two-thirds the maximum width across the anterior wings. There is a distinct lateral notch, and the shoulders are sharply pointed, the tip directed ventrally. The doublure is widest near the shoulder, the inner edge extended in a small ventrally-directed posterior wing. There is a circular hole through the doublure at the shoulder. Posteriorly the doublure is narrowest. Ornament of granules, but coarse tubercles on tips of crescent-shaped posterior lobe of middle body, and along posterior margin.

Segments from all parts of thorax now known (Pl. 3, figs. 11, 12, 15, 16) but not complete number. The anterior segment (Pl. 3, fig. 11), since it fits behind the cephalon, lacks the anterior, and has an extremely short posterior, pleural spine. The articulating half ring is, however, larger and more convex than that of posterior segments. The photographs show the progressive increase in size of both pleural spines in successive segments, as well as the changes in direction.

Axis of the pygidium (Pl. 3, fig. 19) with two rings and a pair of spines at the tip, suggestive of a third segment. The base of the large, upwardly directed spine on the margin of the pleural region is situated between the bases of the 3rd and 4th pleural spines, and is connected by a low ridge to the first axial ring.

Photographs at high magnifications (Pl. 9, fig. 6) show the dorsal external surface of the exoskeleton covered with symmetrically situated thorn-like spines with granules between. The granulation is absent only from the posterior edge of the

Figure 9. *Diacanthaspis cooperi* Whittington. A, B, Protaspis, dorsal and ventral views, drawn from the original of Plate 3, figures 1, 2. In A, the right free cheek has been drawn in its correct position rather than displaced as in B and the original. In B, the outline of the poorly preserved hypostome is indicated by a broken line. C, Stage 0 exoskeleton with only right free cheek restored in position. Drawn from original of Plate 3, figure 3, and free cheek of appropriate size. D, small cranidium and left free cheek drawn from originals of Plate 3, figure 8. Approximately X 62. Paired spines numbered and lettered as in Text-figure 1; Lb is librigenal.

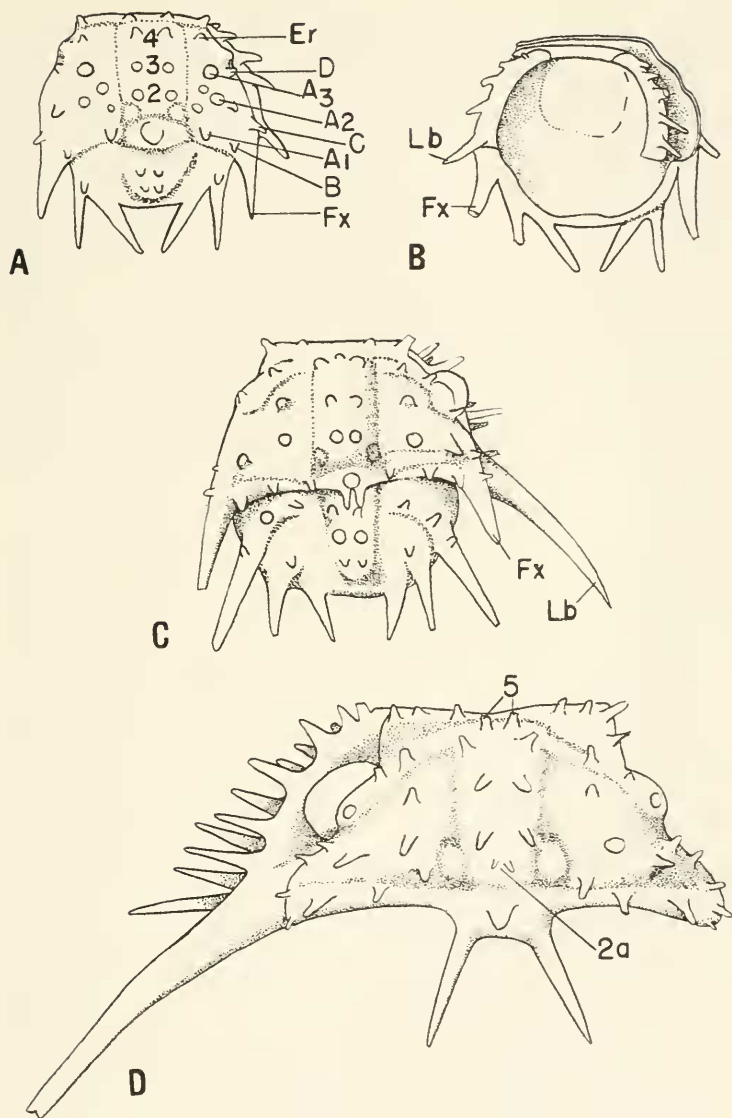


Figure 9

occipital ring, the upper part of the posterior cephalic border, corresponding edge of the thoracic axial rings and the posterior pleural bands, the border of the pygidium and the raised ridge on the pleural regions, and the paired occipital, librigenal, and posterior pleural spines. Distally directed openings may be seen on the occipital and librigenal spines, and between and on the granules at the tips of the lateral cephalic and pygidial border spines openings were present (Pl. 11, fig. 16). The thorn-like spines, when not obviously broken, appear bluntly rounded at the tip, with a distinct, tiny central opening surrounded by an irregular ring of tiny depressions or openings (Pl. 9, fig. 6). The median occipital tubercle is short and bluntly rounded at the tip, and some specimens show four depressions, arranged in a square, on the slopes of the tip (Pl. 11, fig. 18). These appear to be depressions, not openings through the exoskeleton, and resemble those seen in, for example, *D. aff. ulrichi* n.sp. and *D. orandensis* n.sp. (see below).

Development: Protaspis (Pl. 3, figs. 1, 2, 5, 6; Text-fig. 9 A, B) of length (sag.) 0.42 mm., maximum width (tr.) at base of fixigenal spines 0.51 mm. Shield subcircular in outline, gently convex, most strongly so anteriorly; divided by faint, curving transverse furrow into larger cephalic and smaller pygidial portion; doublure narrowest posteriorly. Glabella outlined by broad, shallow furrows, gently convex, a median occipital and three pairs (2, 3 and 4 of Text-fig. 9A) of axial spines; occipital furrow faint, in front of outer parts pair of extremely faintly defined, subcircular, basal lateral lobes. Cheeks slope quite steeply antero-laterally, connected by narrow anterior border; low eye lobe far forward and outward, almost in line with axial spines 4. Eye surface not preserved. Free cheek narrow, the two branches of the suture forming a straight line on the dorsal side, curving across the doublure as shown in Text-figure 9B. Posterior border not clearly defined, extended into long, broad-based fixigenal spine. Short spines or tubercles arranged symmetrically on cheeks and anterior border include A_1 , A_2 , A_3 , B, C, D, Er, two pairs on the anterior border, and additional small tubercles on the fixed cheek. Five spines on vertical margin of free cheek, posterior (librigenal) the longest. Protopygidium with strongly convex axis, especially posteriorly, bearing two pairs of tubercles. Pleural regions depressed near

axis, convex toward rolled border; two stout pairs of border spines, outer pair with spine at base, inner pair directed backward and inward. Rostrum and hypostome poorly preserved (Pl. 3, fig. 2), general outline as suggested in Text-figure 9B.

Exoskeleton at Stage 0 (Pl. 3, figs. 3, 4; Text-fig. 9C) of length (sag.) 0.57 mm., width (tr.) at base fixigenal spines 0.6 mm., length (sag.) of cephalon 0.34 mm. A dissociated free cheek of appropriate size has been drawn in position in Text-figure 9C. Glabella parallel-sided, more convex, defined by deep axial furrows; deeper occipital furrow and ring relatively wider, with large median tubercle and slimmer but longer paired spines; low median tubercle in front of axial spines 4. Tiny basal lateral glabellar lobe faint, almost concealed by increased inflation. Cheek more convex, eye lobe larger and farther back, course of cephalic suture similar. Posterior border defined distally, fixigenal spines as long as in protaspis. Tubercles (or short spines) as on protaspis, on posterior border additional spine between A_1 and B. Free cheek with librigenal spine stouter and longer than fixigenal, five spines on edge of border, decreasing in size forward. A new row of spines has appeared on the border, outside and below the other, directed outward and downward, extending to base of librigenal spine and increasing in length posteriorly. Transitory pygidium (width (tr.) at anterior margin 0.5 mm.) with well-defined axis, pleural regions flat with rolled border. Three pairs of spines on axis, and three on borders, inner directed slightly inward. First interpleural furrow faint, two spines on pleura, outer at base of border spine, third small spine on outer side border spine near base. Upright spine at base second border spine.

Smallest cranidium previously described (Whittington, 1941, Pl. 74, fig. 1; text-fig. 2) slightly larger than those of Stage 0, and without trace of fixigenal spines. A cephalon of length (sag.) 0.51 mm. is here restored (Text-fig. 9D; Pl. 3, fig. 8) and is at same stage of development as original of my 1941, Plate 74, fig. 2 and text-figure 3. Basal part of glabella wider, basal glabellar lobes much larger, axial spines 2a have appeared, as have axial spines 5 (in place of the median tubercle of Stage 0). Eye lobe larger and farther back, but most striking is absence of fixigenal spine, so that librigenal spine is at genal angle.

There are no specimens showing any transition (e.g. a reduction of the genal spines) between Stage 0 and this stage.

The smallest transitory pygidium previously described (Whittington, 1941, p. 508; Pl. 74, fig. 11) is probably that of Stage 1, while the larger one (op. cit., p. 508; Pl. 74, fig. 12, 13) may belong to a stage between 1 and 8. A new specimen (Pl. 3, figs. 17, 18) appears to belong to Stage 8 (assuming that the holaspis thorax is composed of 10 segments). Anterior segment defined by interpleural groove, and right posterior pleural spine curves backward and slightly inward. Proximal portions of the posterior pleural spines of second segment may be seen, and inside them there are four pairs of small marginal spines. On the right side (the left is broken off), just inside the margin, is a long upwardly and backwardly directed spine, its base in line with the fourth pair of spines on the axis. The inclination of this spine is different from that of the posterior pleural spines, and it appears to be the upwardly directed major pleural spine so characteristic of the true pygidium. On the posterior pleural bands of the first two segments are two short spines, upwardly directed, the outer at the base of the posterior pleural spine, and forming a curved line between the axial ring and posterior pleural spine. A spine corresponding to this outer spine is present on the pleural portion of the third segment, just in front of the upwardly directed major pleural spine. The curve between the axis and the base of the major spine corresponds with that of the first two segments, and suggests that the major pleural spine is the modified posterior pleural spine of the first segment of the true pygidium.

DIACANTHASPIS LEPIDUS Whittington, n.sp.

Plates 4, 5; Plate 7, figure 15; Text-figures 8, 10

Holotype: USNM 116517 (Pl. 5, figs. 1, 4, 7, 9), locality 2.

Other Material: Paratypes USNM 116518 a-c; all figured specimens in USNM.

Geological Horizon and Localities: lower Edinburg limestone, localities 2, 3, 4.

Description: At the localities given above, two species of *Diacanthaspis* occur, *D. lepidus* n.sp., and *D. secretus* n.sp., the

latter described below. Material from these localities, collected at different times, has been prepared, and the relative frequency of occurrence of parts of the adult exoskeleton is as follows (counts of complete or nearly complete parts only):

TABLE 1
Numbers of Exoskeletal Parts of Two Species of
Diacanthaspis at Localities 2-4.

	Locality 2	Locality 3		Locality 4
	Cooper Collection	Evitt Collection	Cooper and Whittington Collection	Evitt and Whittington Collection
<i>D. lepidus</i> n.sp.				
Cranidia	41	112	45	14
Free cheeks	48	185	20	8
Pygidia	78	122	12	14
<i>D. secretus</i> n.sp.				
Cranidia	57	24	4	14
Free cheeks	75	30	—	15
Pygidia	98	14	—	12

The rarity of *D. secretus* at locality 3, and the fit of the free cheeks, has led to the associations made here (Text-fig. 8), and support is afforded particularly by the nature of the ornament. No specimens are intermediate in morphology between those here called *D. lepidus* and *D. secretus*, and there is little variation in even minor features of the ornament between individuals of either species. It might be suggested that these two morphological types, occurring together, are sexual dimorphs of one species, rather than two distinct species. The fact that *D. secretus* is rare at locality 3, but occurs in almost equal numbers to those of *D. lepidus* at localities 2 and 4, seems to argue against this suggestion.

Diacanthaspis lepidus is considerably older than the type species, *D. cooperi*, and is distinguished from it at once in lacking the

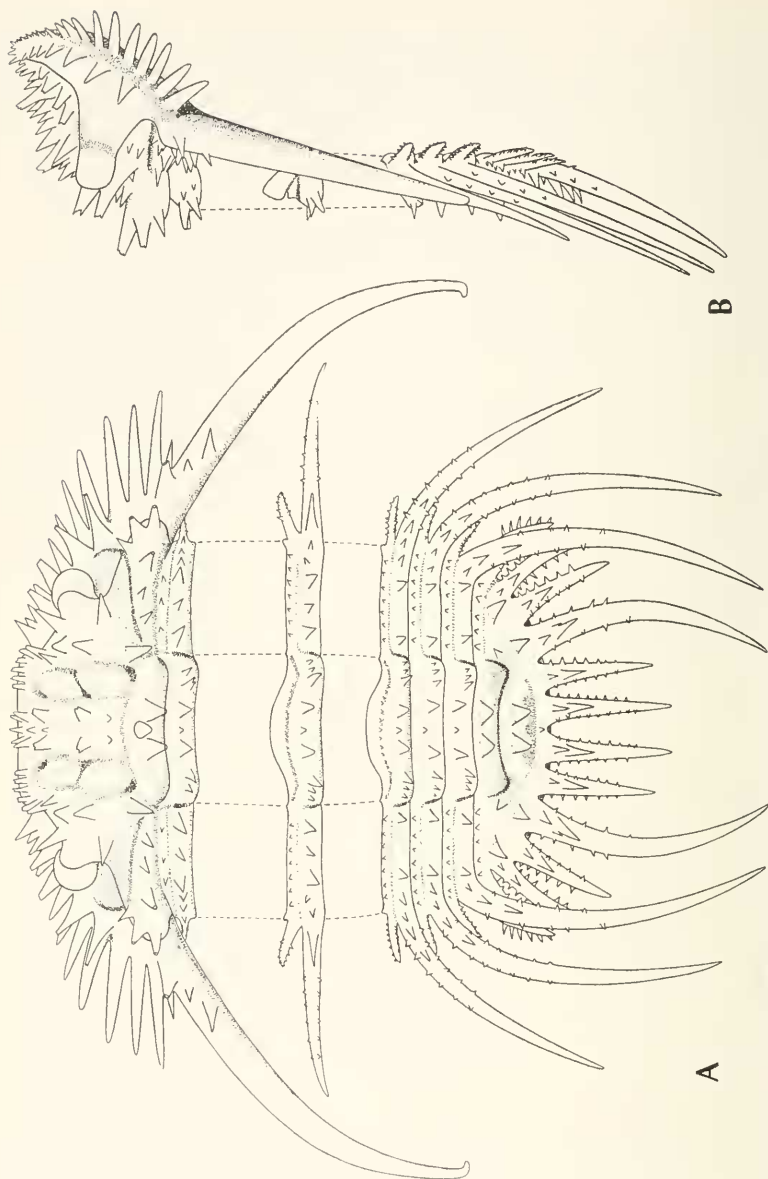


Figure 10. *Diacanthaspis lepidus* n.sp. Reconstruction, A, dorsal, B, right lateral views. Number of thoracic segments unknown. Approximately X 12.

stout occipital spines. The cephalon is less convex transversely, and both the width (tr.) between the palpebral lobes, and of the occipital ring, are lesser fractions of the cranial width. Occipital lobes are absent. Tip of librigenal spine hooked. The pygidium of *D. lepidus* is relatively shorter than that of *D. cooperi*, and has the elongated fourth marginal spines. That of *D. cooperi* has a long upwardly-directed spine situated on the border inside the base of the fourth marginal spine, which latter is not elongated. One hypostome from locality 3 is referred to *D. lepidus*, since this is the common species at this locality. It is of the same general type as that of *D. cooperi* (compare Pl. 3, figs. 7, 9, 10 with Pl. 5, figs. 15-17), but different in detail — e.g. the outline of the lateral and posterior margins, depth of lateral notch, projection of shoulder directed laterally rather than ventrally, greater convexity of middle body, and shorter middle furrows. The doublure is incomplete postero-laterally, but at the shoulders it shows no circular opening.

The long thorn-like spines on the external surface are hollow, and the tips of even the longest and best preserved are not pointed, but cut off (Pl. 7, fig. 15). The end is usually open, but in some is covered by a plate having several tiny holes or depressions in it (Pl. 4, fig. 22). Openings, directed distally, occur on the librigenal spines, tips of the cephalic outer border spines, on the posterior pleural spines of the thorax, and near the tips of the pygidial border spines. These openings may have been occupied by sensory hairs. On the cephalon, between the thorn-like spines, the external surface is granulate, except on the convex surface of the borders and occipital ring. Similarly, granulation is absent from the convex surface of the axial rings, the posterior pleural bands, and the border of the pygidium.

Development: A series of cranidia down to the length (sag.) 0.48 mm. is shown in Plate 4, figures 8-10, 12-14, 16-18. The smallest (Pl. 4, fig. 6) is distinguished from that of a smaller size of *D. secretus* n.sp. (Pl. 6, fig. 12; Text-fig. 11C) by the presence of a median, as well as small paired, occipital spines, faint basal glabellar lobes, a less marked indentation in the anterior margin, a slightly different arrangement of the spines on the fixed cheek on and inside the palpebral lobe (spines A_2 , A_3 , D, and Er), and a tiny additional spine at the extremity

of the posterior border near the posterior edge, between spines B and C. In cranidia of 0.5-0.66 mm. in length (compare Pl. 4, fig. 7, with Pl. 6, figs. 14, 15), some of these differences are more pronounced — the smaller indentation in the anterior margin in *D. lepidus*, the different arrangement of the spines referred to on the fixed cheek and the additional spine on the posterior border. The first two of these differences persist into larger sizes, and aid in differentiating the species. Another specific character already evident at this size is the different shape of the palpebral lobe. In larger cranidia the differences between *D. lepidus* and *D. secretus* become more pronounced.

All the tiny cranidia with fixigenal spines (probably Stage 0) known from localities 3 and 4 are of the type shown in Plate 6, figures 6, 7 (cf. Text-fig. 11B), i.e. all the spines are long, with a thick base and bluntly terminated tip, there is a single occipital and axial pairs 2, 3, and 4, and the anterior margin is indented. This type is so like the cranidial portion of the protaspis from locality 4 shown in Plate 6, figures 1-5 that the conclusion that they form part of a series is inevitable, and this series is traced into the holaspis *D. secretus*. However, a second protaspis known from locality 4 (Pl. 4, figs. 1-5) is clearly odontopleurid, and differs from that of *D. secretus* only in the following characters: (a) the spines on the dorsal surface are low, appearing rather as high tubercles; (b) the occipital ring bears a median spine and a suggestion of small, paired spines just behind the median spine; (c) small basal glabellar lobes are present; (d) axial spines 5 are represented by tiny tubercles. The characters (a), (b), and (c) are those which distinguish the smallest known cranidium of *D. lepidus*, the spines on the external surface being less massive than those of *D. secretus*. Axial paired spines 5 are not known in this size of *D. lepidus* cranidium, but there is a median axial 5. This second protaspis from locality 4 is thus tentatively regarded as that of *D. lepidus*, for comparison between it and smallest known cranidia of other species of *Diacanthaspis*, and of *Ceratocephala*, *Apianurus* n.gen., and *Calipernurus* n.gen., reveals far greater differences.

DIACANTHASPIS SECRETUS Whittington, n.sp.

Plate 6; Plate 7, figures 1-14; Text-figures 8, 11.

Holotype: USNM 116519 (Pl. 7, figs. 1, 3, 5, 11), locality 2.

Other Material: Paratypes USNM 116520 a-d; all figured specimens in USNM.

Geological Horizon and Localities: lower Edinburg limestone, localities 2, 3, 4.

Description: The occurrence of this species is discussed under *D. lepidus* n.sp. The seemingly minor but persistent differences that distinguish *D. secretus* from *D. lepidus*, summarized in Text-figure 8, are: 1) the longer, lower palpebral lobe, more strongly curved course of the anterior branch of the suture, and better-defined eye-ridge (compare Pl. 5, figs. 1, 4, 7, with Pl. 7, figs. 1, 3, 5); 2) the different direction and arrangement of the four long spines on the fixed cheek between the palpebral and lateral glabellar lobes (compare Pl. 5, fig. 1 with Pl. 7, fig. 1); 3) the backward curve of the tips of the outer spines on the border of the free cheek, and the lesser number of spines on the upper surface of this border (compare Pl. 5, fig. 9 with Pl. 7, fig. 7); 4) the relatively longer pygidium, in which the fourth marginal spines are not elongated (compare Pl. 5, fig. 12 with Pl. 7, fig. 10). A single small ornamental spine, upwardly directed, is present at the base of the 4th, 5th, and 6th marginal spines: in *D. lepidus* two such spines are present on the 3rd, 4th, 5th, and 6th marginal spines. Other ways in which the exoskeletal parts of the two species can be discriminated may be seen from a study of Plates 5 and 7. It will be seen that the minor ornamental spines of *D. lepidus* tend to be longer and sharper, as well as more numerous in certain regions (compare Pl. 5, figs. 1, 7, 9 with Pl. 7, figs. 1, 3). The thorax of neither species is completely known, but isolated segments of *D. secretus* have shorter, blunter ornamental spines, and the lateral barbs on the anterior pleural spine are fewer (compare Pl. 5, figs. 2, 3, 10, 11 with Pl. 7, figs. 4, 6).

The librigenal, cephalic, thoracic pleural and pygidial border spines of the exoskeleton show openings (Pl. 7, figs. 12-14) like those described in *D. lepidus*. The thorn-like spines have the tips cut off and closed, with tiny openings or pits in the end. The granulation is distributed as in *D. lepidus*. Intermediate between the thorn-like spines and granules are high tubercles, and these apparently are closed at the tip.

Development: Metaprotaspis (Pl. 6, figs. 1-5; Text-fig. 11A)

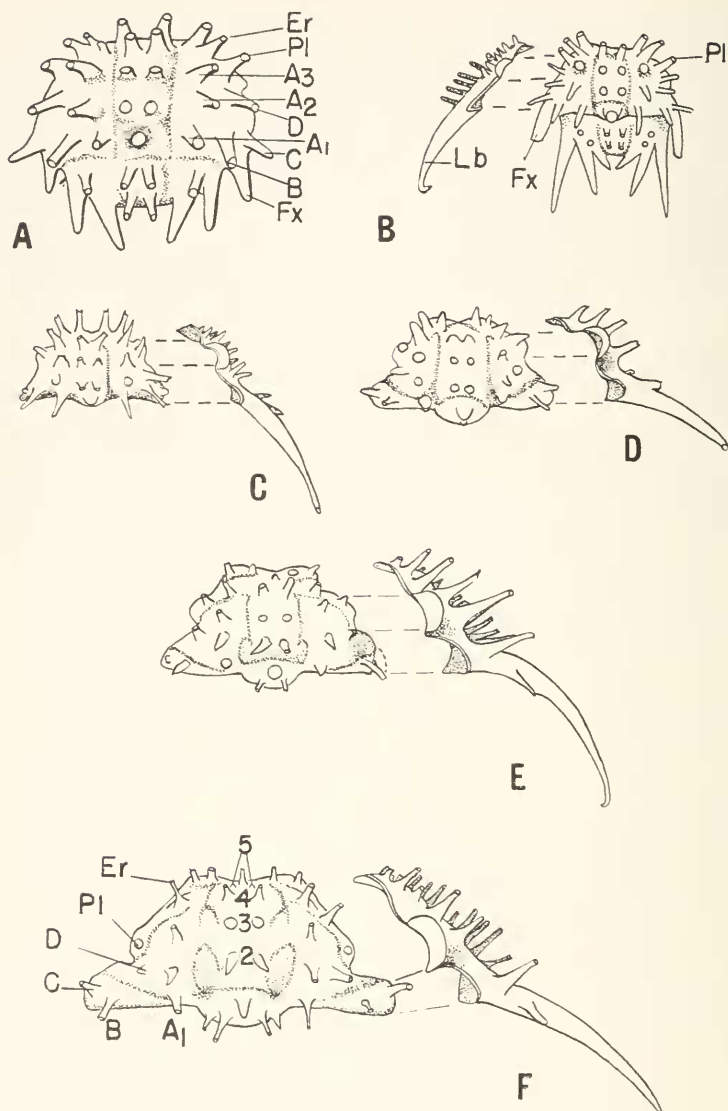


Figure 11

subcircular in outline, gently convex; free cheeks, rostrum and hypostome unknown. Cranidial portion divided by shallow, broad, poorly-defined axial furrows into glabella, with very gentle convexity, and gently convex fixed cheeks. Glabella not divided into rings, but with stout median occipital spine and three pairs in front, a fourth pair on the anterior border, these four pairs forming two lines diverging slightly forward. Posterior area of cheek with prominent spines on dorsal surface symmetrically arranged, lettered A_1 , A_2 , A_3 , B, C, D, in Text-figure 11A. At margin, at end of curving row formed by median occipital and spines A_1 and B, is posteriorly directed fixigenal spine. On anterior area of cheek, spines included are those labelled Pl, A_3 , and Er respectively in Text-figure 11A, and one on anterior border. Anterior margin faintly indented at midline. Only a gentle slope divides cranidium from protopygidium. Axis prominent, two pairs of spines, two horizontal pairs directed back from margin of pleural regions, and one pair on dorsal surface at base anterior marginal spine.

Stage 0 specimen reconstructed (Text-fig. 11B) from originals of Plate 6, figures 6, 10, and similar specimens. It is larger in size (length (sag.) about 0.5 mm., length cranidium 0.32 mm.) but otherwise exceedingly similar, except for the presence of a third pair of border spines on the pygidium. Free cheek extremely narrow (tr.), small eye lobe far forward, row of five spines on upper surface of convex border, row of seven on outer surface of border, long librigenal spine with hooked tip. Rostrum and hypostome unknown. Text-figures 11C-F (cf. Pl. 6, figs. 8, 12, 14, 15) show larger cranidia and associated free cheeks. Not until the cephalon is about 0.5 mm. in length (sag.) (Text-fig. 11E, Pl. 6, fig. 14) do small paired occipital spines appear, faint

Figure 11. *Diacanthaspis secretus* n.sp. A, Protaspis, dorsal view, drawn from the original of Plate 6, figures 1-4. Approximately X 52. B, Stage 0, dorsal view, left free cheek separated from cranidium, drawn from originals of Plate 6, figures 6, 10. Approximately X 32. C, D, E, F, cranidium and right free cheek of individuals of increasingly larger size, exterior views. Drawn from originals of Plate 6, figures 8, 9, 12, 14, 15 respectively. Approximately X 32. Paired spines numbered and lettered as in Text-figure 1; Lb is librigenal.

basal glabellar lobes, and a median axial spine in front of axial spines 3. The eye has moved back at this stage, and considerably farther back at the next stage shown, when the second lateral glabellar lobes and axial spines 5 appear (Text-fig. 11F; Pl. 6, fig. 15). The indentation in the anterior margin is marked in small cranidia but becomes much less obvious, though not quite obliterated, as size increases. Additional paired spines appear on cranidia of length (sag.) about 1 mm. (Pl. 6, fig. 16) upwards. A slightly larger transitory pygidium than Stage 0 (Pl. 6, fig. 13) has three pairs of spines on the axis, the border with three pairs of spines directed horizontally (posterior pleural spines), progressively shorter backward. At the antero-lateral corner is the broken base of a tiny anterior pleural spine. On the pleural region a short spine is situated at the base of the first two posterior pleural spines, remainder of region granulated, and showing the first pleural furrow and interpleural groove. A considerably larger transitory pygidium (Pl. 6, fig. 20) shows 4 pairs of axial spines and 4 posterior pleural spines. Short, blade-like anterior pleural spines are present on the first three segments (mostly concealed in dorsal view); there are two spines on the posterior pleural band of the first segment, the outer one longest.

Discussion of Ontogeny of *Diacanthaspis*

If these ontogenetic series of *D. lepidus* and *D. secretus* be accepted, it is remarkable that the protaspis of the latter (Pl. 6, figs. 1-5) has far the more massive and prominent spines on the external surface, while the reverse is the case in the holaspis, where the spines, though massive, are fewer and shorter and thus less prominent than the long, thin, thorn-like spines of *D. lepidus* (compare Pl. 7, figs. 3, 15). Comparison of the metaprotaspis and Stage 0 specimens of *D. lepidus* and *D. secretus* with corresponding specimens of *D. cooperi* (Pl. 3, figs. 1-6; Text-figs. 9A-C) reveals the close similarity — in outline and form, shape of glabella, presence of fixigenal spines, number and arrangement of spines on the external surface, and axial and border spines of the protopygidium. Distinctive of *D. secretus* is the size of the spines on the external surface, while in both the others these spines are short and rounded. In *D. lepidus* and

D. cooperi basal glabellar lobes are present in the metaprotaspis. Comparison between later developmental stages (Pl. 4, figs. 6-10, 12-14, 16-18; Text-figs. 9D, 11C-F; Whittington, 1941, text-figs. 2-6) reveals both the parallelisms and specific divergence. Fixigenal spines are lost abruptly in all. In *D. secretus* lateral glabellar lobes and axial spines 2a and 5 appear at a later stage than in either of the other species. While paired spines are present on the occipital ring of the older species, they never become bigger than the median occipital tubercle, whereas in *D. cooperi* their growth is rapid.

DIACANTHASPIS ULRICHI Whittington, n.sp.

Plate 8; Text-figures 8, 12.

Holotype: USNM 116521 (Pl. 8, figs. 1-5), locality 7.

Other Material: Paratypes USNM 116522a-c: all figured specimens in USNM.

Geological Horizon and Localities: lower Edinburg limestone, localities 3, 4, 7. This species has not been found at locality 2, and only 2 pygidia are known from locality 3. From locality 4, 8 cranidia and 14 pygidia, together with 26 immature cranidia, have been recovered. At locality 7 *D. ulrichi* is not accompanied by *D. lepidus* and *D. secretus*, whereas at locality 4 these latter two species are rather more abundant (see Table 1, p. 217) than is *D. ulrichi*.

Description: *D. ulrichi* is readily distinguished from contemporary and later species (except *D. aff. ulrichi*) by: (1) the convex fronto-median glabellar lobe and narrow (tr.), low lateral lobes, which latter are separated from the fixed cheeks by extremely faint axial furrows; (2) the straight course of each branch of the suture adjacent to the eye lobe, which gives a distinctive outline to both cranidium and free cheek; (3) the short, thick, bluntly terminated median and paired main occipital spines; (4) the convex axis and outwardly-sloping pleural regions of the pygidium; (5) the short spines on the outer edge of the cheek border and border of the pygidium.

The external surface of the cephalon (Pl. 8, figs. 24, 30) bears, besides the main occipital and outer border spines referred to, smaller, thick, blunt-tipped spines. Inside the cephalic

borders the surface between the spines is covered with fine granules. The blunt spines are symmetrically arranged on the lateral glabellar lobes and cheeks, but on the fronto-median lobe, while the number and general disposition is similar in different specimens, it is not exactly the same, nor is the arrangement symmetrical (Pl. 8, figs. 1, 30). On the posterior edge of the occipital ring (Pl. 8, fig. 24) there is a median and a pair of these spines, and in some specimens a second pair is situated in front of the main pair.

Hypostome unknown.

Pleurae of thoracic segments (Pl. 8, figs. 12, 13, 17, 21) with narrow (exs.) anterior and wide (exs.) posterior band, former bearing short anterior pleural spine, latter bearing larger spine, progressively longer and more backwardly curved on successive segments. Axis with 2 pairs spines, 3 on posterior band, area between smooth; articulating groove, anterior band, and posterior flange tuberculate. Axis of pygidium with two rings, each with pair of spines. Six pairs of spines on outer edge of border, the first very small, the fourth elongated and connected by a low ridge to the first axial ring. Prominent spine on upper surface of border at base of elongated fourth spine. One specimen (Pl. 8, fig. 9) has only one, rather than two, pairs of spines between the major border pair.

The distal portions of the main median and paired occipital spines (Pl. 8, figs. 24, 30) display an irregular, hummocky surface at high magnifications. There may have been openings at the base of the tubercles on the paired spines, and the tip of the median spine shows the four tiny depressions arranged in a square. The distal tips of the posterior outer border spines of the free cheek, and the longer border spines of the pygidium, may have been like those of the paired occipital spines. Other, shorter, spines are rounded at the tip and may be closed, and the distal part of the librigenal spine does not show any openings.

Development: Protaspis unknown. Development of cephalon from Stage 0 shown in Text-figure 12 A-D (compare Pl. 8, figs. 10, 14-16). The smallest cranidium has the characteristic trapezoidal outline, low, parallel-sided glabella divided only by the occipital furrow, low palpebral lobe far forward, faint eye ridge, and fixigenal spine. The presence of the latter suggests

that it belongs to Stage 0. The median occipital spine is represented by a large, low tubercle, and the paired occipital spines, present in some specimens of this size, are tiny. Remainder of glabella without paired spines. On fixed cheeks paired spines A_1 , A_2 , A_3 , B, and C have been recognized. Surface of cranidium between spines covered with fine granules. In the next size of cranidium found, fixigenal spines are absent, the palpebral lobe is farther back, and paired spines 2, 3, 4 appear on the glabella

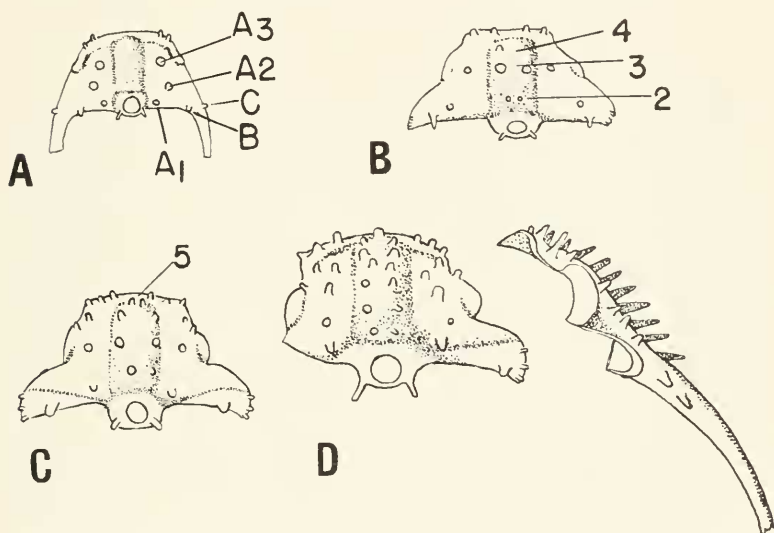


Figure 12. *Diacanthaspis ulrichi* n.sp. A, B, C, D, cranidia of increasing size, exterior views, right free cheek shown in D. Approximately X 38. Drawn from the originals of Plate 8, figures 10, 14, 15, 16, 28 respectively. Paired spines numbered and lettered as in Text-figure 1.

in front of the occipital furrow. At this stage the cranidium is quite like that of *D. cooperi* (Whittington, 1941, text-fig. 2) and *D. secretus* (Pl. 6, fig. 12; Text-fig. 11D), but the large median occipital tubercle and fewer and shorter paired spines on fixed cheeks and borders are distinctive. The later development parallels that of other species, except that beyond a length (sag.) of about 0.6 mm. the symmetrical arrangement of spines on the glabella in front of the occipital ring is lost.

On Plate 8, figures 25, 26 show a transitory pygidium of an unknown stage. Axis with three pairs of spines; two long border spines are posterior pleural spines of two segments that will be released into thorax; anterior pleural spine of first is short, curved. Behind axis, two pairs of tiny border spines. A small holaspid pygidium is shown in Plate 8, figures 22, 23.

DIACANTHASPIS aff. ULRICHI Whittington, n.sp.

Plate 9, figures 1-5, 7-9; Text-figure 8.

Material: all figured specimens in USNM.

Geological Horizon and Localities: Oranda formation, locality 8.

Description: a few fragments only of this extremely rare species are known, and deemed insufficient as the basis for a new specific name. It is like *D. ulrichi* n.sp., but differs (compare Pl. 9, figs. 1, 5, with Pl. 8, figs. 1, 6), for example, in the more convex fronto-median glabellar lobe, the longer median occipital spine, the deeper axial furrows of the cranidium, particularly outside the lateral glabellar lobes, and the more triangular outline of the pygidium. The spines and granules on the external surface of the two species are similar both in appearance and distribution (compare Pl. 9, figs. 7-9 with Pl. 8, figs. 24, 30). The smooth tip of the median occipital spine shows clearly the four depressions arranged in a square. The smooth, blunt tips of the spines on the glabella and free cheeks show a tiny central opening.

DIACANTHASPIS ORANDENSIS Whittington, n.sp.

Plate 10; Pl. 11, figures 1-15, 19, 20; Text-figure 8.

Holotype: USNM 116523 (Pl. 10, figs. 1, 3, 5-7), locality 8.

Other Material: Paratypes USNM 116524a-f; all figured specimens in USNM.

Geological Horizon and Locality: Oranda formation, locality 8.

Three species occur at this locality, and approximate numbers of complete or fairly complete parts of exoskeletons obtained are as follows:

TABLE 2

Numbers of Exoskeletal Parts of Three Species of
Diacanthaspis at Locality 8.

	<i>D. orandensis</i> n.sp.	<i>D. scitulus</i> n.sp.	<i>D. aff. ulrichi</i> n.sp.
Cranidia	120	25	2
Free cheeks	150	38	1
Pygidia	100	31	2

The most common hypostome, 130 specimens, is regarded as belonging to *D. orandensis*, the less common, 16 specimens, to *D. scitulus*.

Description: *Diacanthaspis orandensis* is exceedingly similar to *D. cooperi*, differing only in minor but persistent characters, of which the more obvious are: (1) relatively longer outer border spines on free cheek and pygidium (compare Pl. 10, figs. 2, 17, 18, with Pl. 3, fig. 19, and Whittington, 1941, Pl. 74, fig. 23); (2) more prominent axis of pygidium; (3) thorn-like spines on external surface tend to be longer and sharper; (4) particularly axial, but also longitudinal, furrows bounding first and second lateral glabellar lobes tend to be deeper and lobes to be more prominent (compare Pl. 10, figs. 1, 3, 5; Pl. 11, fig. 19 with Pl. 9, fig. 6, and Whittington, 1941, Pl. 74, figs. 24, 25, 29). As might be expected, the early developmental stages of the two species are indistinguishable (compare Pl. 11, fig. 1 with Pl. 3, fig. 8); only later do the specific differences become clear.

No complete specimens of the librigenal spines are known, i.e. the extreme tip is always broken, but almost certainly it is not hooked. The dorsal external surface of *D. cooperi* has been described in detail, and most of the remarks apply to *D. orandensis*. Specimens of the latter, however, are better preserved, and there is no doubt of the presence of distally-directed openings, with raised rims, on the paired occipital, librigenal, posterior pleural, and pygidial border spines. On the rounded tip of the median occipital spine of *D. cooperi* tiny depressions, arranged in a square, were observed. Similar depressions are

present on the occipital spine of *D. orandensis* (Pl. 11, fig. 19), and further, the tips of the thorn-like spines are likewise bluntly rounded with a group of tiny depressions, of which the central may be larger (Pl. 11, fig. 19). The depressions are extremely small, and whether or not they are the openings of canals through the exoskeleton is uncertain.

DIACANTHASPIS SCITULUS Whittington, n. sp.

Plates 12, 13; Text-figure 8.

Holotype: USNM 116525 (Pl. 12, figs. 1-3), locality 8.

Other Material: Paratypes USNM 116526 a-c; all figured specimens in USNM.

Geological Horizon and Localities: Oranda formation, locality 8.

Description: As Table 2 (p. 229) shows, this species is much less common than *D. orandensis* at locality 8. The general plan of the exoskeleton, and particularly the outline of the glabella, absence of prominent paired occipital spines, and arrangement of thorn-like spines on the external surface of the exoskeleton (and particularly of the fixed cheek), ally it with *D. lepidus* n.sp. and *D. secretus* n.sp. rather than with *D. orandensis* and *D. cooperi*. The lack of large median or paired occipital spines, and the form of pygidium, distinguish it from *D. ulrichi*. *D. scitulus* differs from *D. lepidus* and *D. secretus* in that: (1) the cephalon is more convex transversely between the eye lobes, the eye ridges and sutural ridges are stronger and more clearly defined, and the row of border spines on the free cheek extends back onto the base of the librigenal spine (compare Pl. 12, figs. 1-3 with Pl. 5, figs. 1, 7, 9 and Pl. 7, figs. 1, 3); (2) there are seven pairs of horizontally directed border spines on the pygidium, approximately equal in length, and a stouter, longer spine arises from the upper surface of the border and is directed backward and slightly upward (compare Pl. 12, fig. 14 with Pl. 5, fig. 12 and Pl. 7, fig. 10). In the type of major pygidial spine, convexity of the cranidium, strength of sutural ridges, and extension of lateral border spines on to the base of the librigenal spines, *D. scitulus* approaches the *D. orandensis-cooperi* group (compare Pl. 12, figs. 1-3, 14 with Pl. 10, figs. 1, 3, 5, 27). Thus the species of *Diacanthaspis*, while they fall into groups, never-

theless betray their close relationship. Large specimens of *D. scitulus* show, particularly on the inner surface (Pl. 12, fig. 7), a faintly impressed furrow directed transversely on the anterior glabellar lobe where it slopes down to the second glabellar furrow. This furrow is not well enough developed to be termed a third glabellar furrow, but may be the incipient stage of such a furrow. The hypostome is of *Diacanthaspis* type, and distinguished from that of *D. orandensis* (with which it occurs, but in lesser numbers) by the more curved outline of the anterior margin, the less angulate postero-lateral outline, and the narrower (sag.) posterior border (compare Pl. 13, fig. 8 with Pl. 10, fig. 22). The doublure of the shoulder shows the large circular opening. The one known specimen of the hypostome of *D. lepidus* is of similar type, but does not show the opening through the doublure.

The dorsal external surface of the exoskeleton is shown in Plate 13, figures 12, 14-17. The symmetrically arranged thorn-like spines are truncated and closed at the tip, and there are tiny depressions (which may be openings) in the tip. Granulation extends between the thorn-like spines, but is absent from the cephalic borders, central part of occipital ring and inner corner of fixed cheek around large spine, upper surface of lateral glabellar lobes and eye ridge, axial rings, posterior pleural bands, borders of pygidium and pleural ridge, and border and librigenal spines. Tiny tubercles are present particularly near the tips of the librigenal and border spines. Distally directed openings with a raised rim also occur on the distal parts of these spines, including the tip of the librigenal spine (Pl. 13, fig. 14), which is not hooked as in *D. lepidus*, *D. secretus* and *D. ulrichi*.

Development: The smallest known cranidium of *D. scitulus* is 0.93 mm. in length (sag.) (Pl. 13, figs. 3-5), and is very like cranidia of about the same size of *D. lepidus* (Pl. 4, figs. 12-14) and *D. secretus* (Pl. 6, figs. 16-18), even in the size and position of the main thorn-like spines. On the fronto-median glabellar lobe axial spine pairs 2, 3, 4 are present, a median spine only in the position of pairs 2a and 5. On the fixed cheeks spines A₁, A₂, A₃, B, C, and Pl may be seen. The shape of the palpebral lobe, and the strength of the eye ridge and sutural ridges, are especially distinctive of *D. scitulus*, while examples of smaller dif-

ferences are the greater number of spines on the cranidium of *D. lepidus*, and the fewer and differently situated spines of *D. secretus*. The small free cheeks of *D. scitulus* (Pl. 13, fig. 13) have the distinctive border spines, as also do the small pygidia (Pl. 12, fig. 16).

Genus *ACIDASPIS* Murchison, 1839

Text-figure 13.

Synonym (objective) : *Pseudomonaspis* R. and E. Richter, 1917.
Type Species: by monotypy, *Acidaspis brightii* Murchison, 1839
(Whittington, 1956b).

Diagnosis: Two pairs of lateral glabellar lobes well developed, separated from median lobe by deep longitudinal furrows, in type species frontal glabellar lobe rounded, projecting well in front of anterior lateral glabellar lobes. In Ordovician species small third lateral glabellar lobes are present. Median part of occipital ring inflated and prolonged backward as thick median spine, separated from rest of glabella by shallow median part of occipital furrow; lateral part of occipital ring with low, gently convex occipital lobe in inner corner, behind deeper outer part of occipital furrow. Eye lobe elevated, situated opposite most posterior part of basal glabellar lobe; anterior branch of the facial suture runs straight forward and inward, diverging from the course of the eye ridge, crosses border furrow on sutural ridge and curves over the anterior border. Posterior branch curves downward and outward across the fixed cheek in front of the posterior border furrow, and on to the inner side of sutural ridge, against which this furrow ends. It then curves over posterior border, inside base of librigenal spine. Convex anterolateral border with row of stout spines directed downward, longest posteriorly and diminishing forward; antennal notch present, anterior border between sutures projects slightly. Librigenal spines long, curved. Thorax of 10 segments, posterior pleural band convex and inflated at fulcrum. Pygidium with 7 pairs border spines, 5th the major. External surface tuberculate.

Geological Range: Middle Ordovician to Middle Devonian.

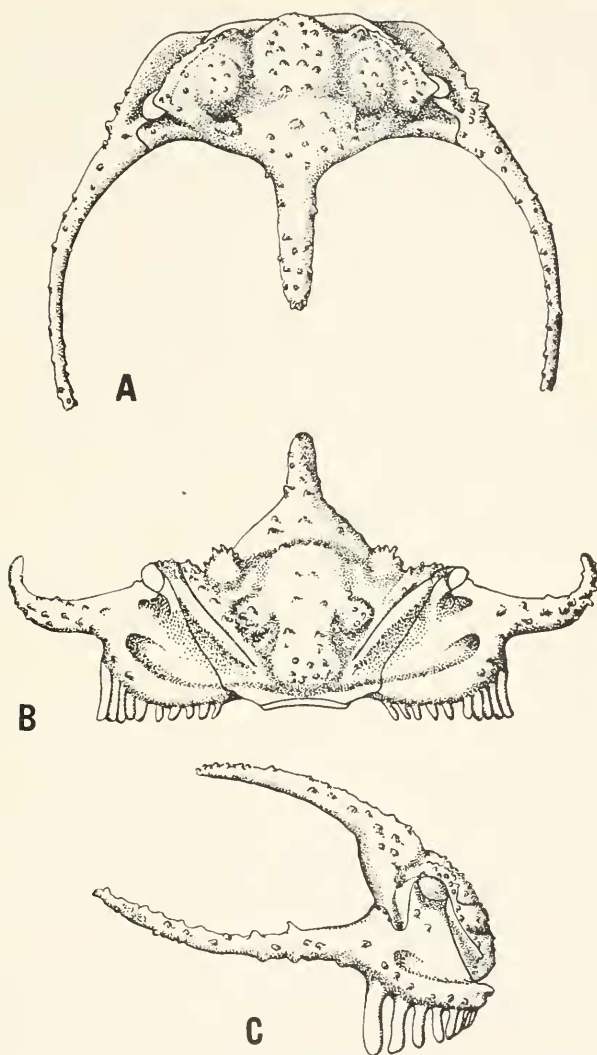


Figure 13. *Acidaspis brightii* Murchison, Wenlock limestone, Middle Silurian, England. A, B, C, cephalon, dorsal, anterior, and right lateral views respectively, approximately X 3. (After Whittington 1956b, text-figure 1.)

Genus *DUDLEYASPIS* Prantl and Přibyl, 1949

Text-figure 14.

Type Species: *Acidaspis quinquespinosa* Lake, 1896
(Whittington, 1956b).

Diagnosis: Occipital ring with short median spine and two further pairs spines on posterior margin; not prolonged back-

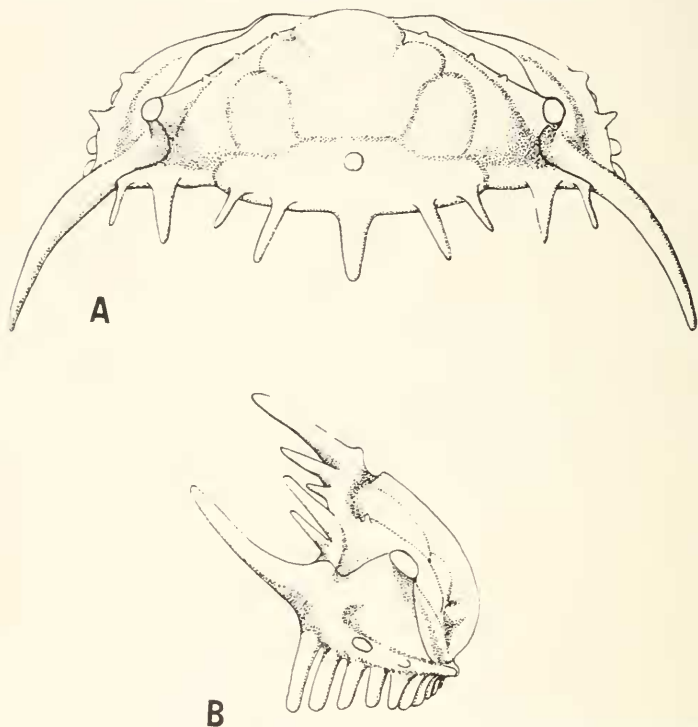


Figure 14. *Dudleyaspis quinquespinosa* (Lake), Wenlock limestone, Middle Silurian, England. A, B, cephalon, dorsal and right lateral views respectively, approximately X 6. After Whittington 1956b, text-figure 2.

ward and lacking lateral lobes. In front of large basal lateral lobes glabella narrows rapidly; small third lobes, third lateral furrows short, transversely directed, frontal glabellar lobe projecting in front of third lobes. Eye lobe situated opposite mid-

part of basal lateral glabellar lobes, anterior branch suture runs on sutural ridge straight forward and slightly inward to anterior border; suture then runs more directly inward and over outer edge of border to meet rostral suture about where anterior border projects forward. Sutural ridge also connects eye lobe and swollen base librigenal spine, and posterior branch suture runs along inner side of this ridge and over border inside base librigenal spine. Convex anterolateral cephalic border with row vertical spines as in *Acidaspis*; librigenal spines slim, curved; two pairs spines on posterior border backwardly directed. Thorax of 10 segments, pygidium with 2 pairs spines between major pair.

Geological Range: Silurian (mainly Middle).

Genus *RADIASPIS* R. and E. Richter, 1917

Type Species: *Arges radiatus* Goldfuss, 1843
(Prantl and Přibyl, 1949, p. 142).

Discussion: The type species has been described by R. and E. Richter (1917, pp. 468-472, text-figs 9, 10; 1926, pp. 109-110; 1930, text-fig. 2). The form of the cephalon is like that of *Acidaspis* — in convexity, lobation of glabella, elongation of occipital ring, presence of lateral border spines, etc., but is distinguished by the paired occipital spines. The thorax is of 9 segments, and the pygidium is notable for the absence of major border spines (there being 8 pairs of equal length) and the bilobed form of the posterior part of the axis. I regard *Radiaspis* as most closely related to *Acidaspis*, not *Odontopleura*, contrary to Prantl and Přibyl's opinion. The genus is known from Lower to earliest Upper Devonian of Germany and Bohemia.

Subfamily *MIRASPINAE* R. and E. Richter, 1917
(=Ceratoccephalidae of Prantl and Přibyl, 1949; of Erben, 1952)

Diagnosis: Glabella wide; occipital ring long (sag. and exs.), convex, with prominent paired spines arising from swollen base; well-defined, sub-parallel sided median lobe, gently to strongly convex, 2 pairs lateral glabellar lobes, small third pair usually present. Convex cheek of characteristic subrectangular outline,

antero-lateral portion projecting, librigenal spine arising from upper surface of border, directed upward and outward, may or may not be spines on cheek border; eye lobe about centrally situated, may be pedunculate; two branches of suture usually inclined to each other at an obtuse angle. Hypostome subrectangular in outline with median posterior notch; middle furrow in form of triangular depression in anterolateral corner of middle body. Thorax of 9-10 segments; pleurae lacking pleural furrow or divided by it into narrow convex anterior and broader convex posterior bands, anterior pleural spine characteristically blade-like, with lateral barbs, and downwardly directed; posterior pleural spine much larger, horizontal, first 2 or 3 directed outward and in some cases slightly forward, successive spines directed more strongly backward. Pygidium with border spines, may or may not be major pair, may or may not be unpaired median posterior border spine.

Geological Range: Middle Ordovician to Middle Devonian.

Discussion: Since this group includes *Miraspis*, the oldest available name Miraspinidae is used for it. Prantl and Přibyl and Erben include here the three best-known genera — *Miraspis*, *Ceratocephala* and *Dicranurus*. As a result of the present study I include *Proceratocephala*, *Whittingtonia*, and *Ceratocephala* (*Ceratocephalina*) n.sub.gen. I have no new information on *Ceratonurus*, *Koněprusia*, *Orphanaspis*, or *Selenopeltoides*, but presume that they may also belong here. It appears to me to be an overestimate of the value of morphological differences to divide this group into three subfamilies, and some of the criteria used by Prantl and Přibyl — e.g. supposed fusion of facial sutures in *Ceratocephala*, lack of anterior pleural spines of thorax in *Dicranurus* — are either of doubtful value or erroneous.

Genus MIRASPIS R. and E. Richter, 1917

Text-figure 15.

Type Species: *Odontopleura mira* Barrande, 1846.

(Whittington, 1956b.)

Diagnosis: Occipital ring with wide (sag.) posterior band. Small third lateral glabellar lobes. Eye lobe situated opposite

mid-part of basal glabellar lobe, pedunculate. Row long, slim spines, diminishing in length forwards, on antero-lateral cephalic border. Nine thoracic segments, well-marked pleural furrow;

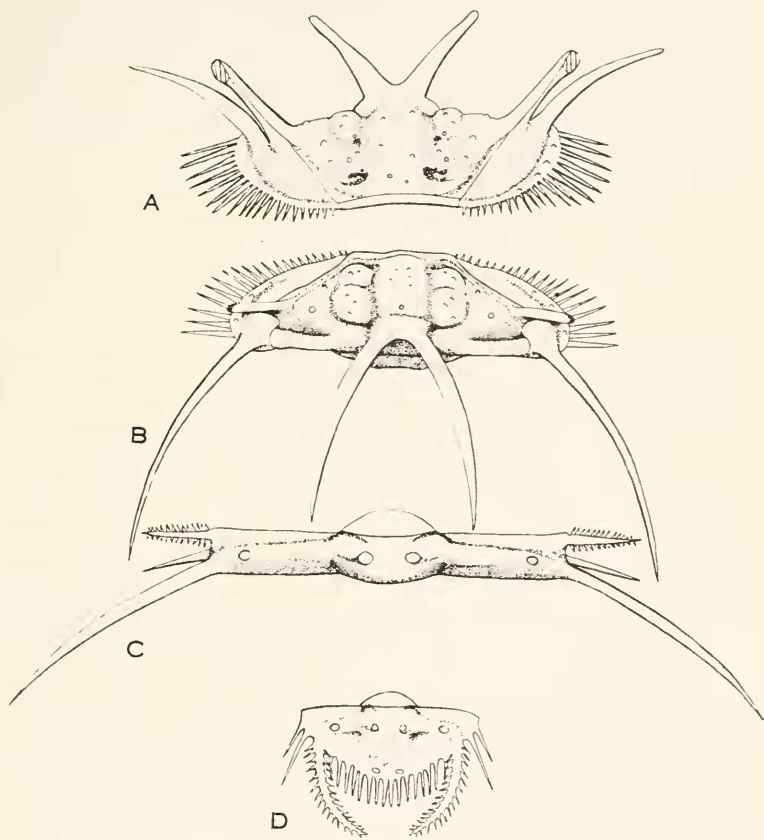


Figure 15. *Miraspis mira* (Barrande), Motol Beds, ea₂, upper middle Silurian, Bohemia. A, B, cephalon, anterior and dorsal views, respectively; C, thoracic segment, dorsal view; D, pygidium, dorsal view. Approximately X 1½. After Whittington 1956b, text-figure 3.

slim additional pleural spine between anterior and posterior. Pygidium with pleural ridge running out at first transversely from first axial ring, then turning abruptly to join base of curved

major spine. Four to eight pairs small border spines between major pair, 2 in front.

Geological Range: Middle (?) Ordovician to Lower Devonian.

Discussion: In addition to the material described elsewhere is the single silicified pygidium discussed below, and the incomplete thorax and *Miraspis*-type pygidium from the Middle Ordovician of Wales (Whittington and Williams, 1955, p. 425, Pl. 40, fig. 119). Complete exoskeletons of Ordovician odontopleurids with *Miraspis*-type pygidium are as yet undescribed, so the range of the genus is uncertain.

?*MIRASPIS* sp.ind.

Plate 14, figures 1, 7.

Material: one incomplete pygidium and one free cheek, both from locality 3, lower Edinburg limestone.

Discussion: The pygidium is of characteristic *Miraspis* form, the short, convex axis with a prominent first ring, bearing a pair of spines. Pleural region crossed by a ridge connected to the axial ring, this ridge directed at first outward and then turning sharply to merge with the base of the major border spine. In front of ridge is first pleural furrow, separating it from low convex band bearing row of three spines. Major border spine long, directed backward and slightly upward, two small spines outside the major spine, 4 pairs inside, upper surface of border with small spines, most prominent pair behind axis. Small spines scattered on pleural regions.

The free cheek has the librigenal spine arising from the upper surface of the border, latter bearing a row of short spines, and the eye lobe is pedunculate. These features recall *Miraspis*, and suggest that possibly this cheek belongs to the same species as the pygidium.

Genus CERATOCEPHALA Warder, 1838

Synonyms (subjective): *Onchaspis* (*Onychaspis*) Raymond, 1925; see Whittington and Evitt, 1954, p. 53. *Trapelocera* Corda, 1847; see Prantl and Přibyl, 1949, pp. 180-181, for summary of argument.

CERATOCEPHALA LACINIATA Whittington and Evitt, 1954

Plate 14, figures 2-6, 8-15; Text-figure 16.

Discussion: Two cranidia from locality 3 (Pl. 14, figs. 2, 3) are smaller (length (sag.) 0.46 and 0.57 mm.; maximum width 0.75 and 0.85 mm. respectively) than those previously described, though not as small as that of *C. triacanthéis* (Whittington and Evitt, 1954, p. 60). They do not have fixigenal spines, but are larger than the cranidia with fixigenal spines of *Apianurus* n.gen. and *Diacanthaspis* described here, and thus seem to represent the immediately succeeding stage when these spines are lost. Notable is the convexity of the glabella of the smallest, on which there are axial pairs of spines 2, 3, and 4 (Text-fig. 16; equivalent

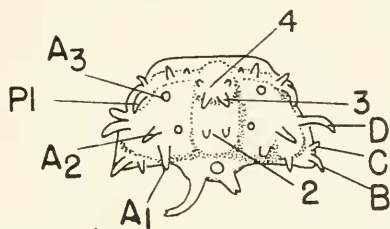


Figure 16. *Ceratocephala laciniata* Whittington and Evitt. Cranidium, exterior view, X 38. Drawn from the original of Plate 14, figure 3. Paired spines numbered and lettered as in Text-figure 1.

to 3, 4, and 5 of Whittington and Evitt, 1954, p. 61, fig. 16), the glabella being highest where spines 3 are situated. Lateral glabellar lobes cannot be distinguished. The palpebral lobe is far forward, bearing a long, curved spine (Pl in Text-fig. 16) and there are three spines on the eye ridge. On the convex fixed cheeks spines A₁, A₂, A₃, B, C, and D may be recognized, and between the spines on both glabella and cheeks there are tiny close-spaced spines. The larger of these two cranidia (Pl. 14, fig. 2) shows characters intermediate between the smaller and the originals of Whittington and Evitt (1954, Pl. 7, figs. 1-8). Pairs of spines 2a, 2, 3, 4, and 5 (equivalent to 2-6 of Whittington and Evitt, 1954, text-fig. 16) are now present on the fronto-median glabellar lobe, as well as a pair on the flanks between 2 and 3.

Basal lateral lobes are faintly developed, and bear a stout median spine, and with this inflation the fixed cheek no longer slopes inward to the axial furrow.

Additional and better-preserved hypostomes (Pl. 14, figs. 11, 12) have shown that the inner edge of the postero-lateral doublure is flexed upward, and just behind the lateral notch it is also thickened. This slight projection may be regarded as the posterior wing. The doublure is flexed (the flexure running almost transversely) at the shoulder, and on the anterior side of the flexure, near the outer edge, a hole pierces the doublure. This hole is present in small hypostomes, is variable in size and usually elongated transversely.

From localities 2, 3, and rarely 4, come the objects shown in Plate 14, figures 5, 6, 10, 13-15. They show a range in size and are both right and left-handed. The two divergent blade-like spines, with a row of thorn-like barbs, curved distally, along each side, are like the anterior thoracic pleural spines and the pygidial border spines of *C. laciniata*. As in these latter spines, there are openings at the tip of the barbs (Pl. 14, fig. 14). The fused base of the two spines is attached to a flat strip which resembles the outer part of a thoracic pleura of *C. laciniata*; it is without a "pleural" furrow, the transverse edge is flattened and bears a row of tiny tubercles along the "upper" edge. The anterior edge of the strip is also very like the anterior edge of the pygidial pleural region, notably in the way the flattened edge slopes forward at the "fuleral articulating process" (Pl. 14, figs. 8, 10). On the opposite ("ventral") side the end of the "pleura" is rolled under and there is an antero-lateral projection ("fuleral articulating process") and a "fuleral" socket beneath the fused base of the spines. When placed as in Plate 14, figures 4, 8, 9, between the outer part of a posterior thoracic segment and a pygidium, the resemblance of this object to the outer part of a pleura is extremely close. Further, the angle made by the lateral margin, and parallel inner margin, of the "doublure," with the sagittal line is a large one, larger than that of an obviously posterior (with backwardly directed posterior pleural spine) thoracic segment. This angle is such as to make the line of the inner edge of the "doublure" fit between that of the pygidium and of a posterior segment, as shown in Plate 14, figure 4. Thus this

object, if it is part of a thoracic pleura, belongs to the posterior thoracic segment. It is not crossed by a pleural furrow, but such furrows, though present in some posterior segments (Whittington and Evitt, 1954, Pl. 6, fig. 6), are extremely shallow and not seen in posterior segments in which the posterior pleural spine points inward and backward. When this object is arranged as in Plate 14, figures 4, 8, 9, it is thus difficult to think of it as anything but the outer part of the posterior thoracic segment. There are difficulties to be surmounted before accepting this conclusion, viz.:

(1) Most serious is the fact that the "pleura" of the object is of constant length and the inner termination is a V-shaped edge, the anterior limb of the "V" the longer, the edge bevelled (Pl. 14, figs. 13, 15). If this object is the distal portion of a segment, why is it terminated in this way, when all other distal parts of segments found are obviously broken (Pl. 14, fig. 4; see also Whittington and Evitt, 1954, Pl. 6, fig. 6)? The flattened edge is like that of the anterior and posterior edges, which would be the sutures between segments. Is the inner edge of this object also a suture? If so these sutures would run symmetrically on either side of an axial ring and innermost pleural parts, a peculiar situation seemingly unique among trilobites. No such median part of this supposed segment has been found.

(2) Why are the two "pleural spines" of the object similar to each other, and not of the distinct anterior and posterior types of all other known segments? The border spines of the pygidium are also of the thoracic anterior pleural spine type, and so, if the object is the outer part of the last segment, it also represents this posterior simplification of spine type.

I have examined two entire specimens of *C. verneuili* in the Museum of Comparative Zoology collections, but they show no peculiar last thoracic segment, and no such segment is illustrated by Barrande (1852, Pl. 38, figs. 5, 6). The objects discussed above occur in material in which *C. laciniata* is fairly abundant, and they also occur in the lower Lincolnshire limestone with *C. triacanthæis* Whittington and Evitt, 1954. *C. rarisipina* n.sp. is not abundant in the Oranda formation, and these objects have not been found at locality 8. Tentatively I regard these objects as part of a thoracic segment of *Ceratocephala*, but the various

problems mentioned above remain at present unsolved. If they are truly distal parts of the last thoracic segment, the reconstruction given by Whittington and Evitt (1954, fig. 13) requires modification on the lines suggested by Plate 14, figure 8.

CERATOCEPHALA RARISPINA Whittington, n.sp.

Plate 15, figures 1-25, 28, 29.

Holotype: USNM 116527 (Pl. 15, figs. 1, 4, 5, 7), locality 8.

Other Material: Paratypes USNM 124698 a-d; all figured specimens in USNM.

Geological Horizon and Locality: Oranda formation, locality 8. This species is rare at locality 8, as shown by the following table:—

TABLE 3

Numbers of Odontopleurid Cranidia at Locality 8.

<i>Diacanthaspis orandensis</i> n.sp.	120
<i>Diacanthaspis scitulus</i> n.sp.	25
<i>Diacanthaspis</i> aff. <i>ulrichi</i> n.sp.	2
<i>Apianurus barbatus</i> n.gen., n.sp.	22
<i>Ceratocephala rarispina</i> n.sp.	7

Description: This species differs from both *Ceratocephala triacanthensis* and *C. laciniata* (Whittington and Evitt, 1954, pp. 54-60, Pls. 6-9, 25, 26, figs. 1-17), bearing perhaps more resemblance to the former, older, species than the latter. Points of discrimination are:—

1) Occipital ring lacks posterior band, and paired spines are more strongly curved outward.

2) Third lateral glabellar lobes not developed.

3) First and second lateral glabellar lobes more inflated and separated from both median lobe and cheeks by well marked furrows.

4) Eye lobe situated farther back than in *C. laciniata*.

5) Border of free cheek subdivided by groove into two convex bands of about same width, both of which merge into base of librigenal spine.

6) Few, larger spines on external surface of cephalon. Six pairs on median glabellar lobe include 2a, 2, 3, 4, 5, the latter being far apart, and an additional pair far apart between 2 and 3. All have counterparts on other two species (e.g. compare Pl. 15, fig. 1, with Whittington and Evitt, 1954, Pl. 8, fig. 1; Pl. 25, fig. 10), as has swollen base of pair 3. Two spines on eye ridge rather than three. Spines along margin of free cheek longer. Conspicuous on *C. rarispina* are the tiny spines that line the edges of occipital furrow and furrows on cheeks (Pl. 15, figs. 1, 29).

7) Hypostome with shallower lateral notch and narrower postero-lateral border.

8) Pygidium with much shorter median border spine.

In *Ceratocephala laciniata* some of the thorn-like spines scattered over the glabella and cheeks appear to have a single opening at the tip (Whittington and Evitt, 1954, p. 59). In at least one specimen of *C. rarispina* (Pl. 15, fig. 28), however, some of these spines are covered over at the truncated tip, there being several minute depressions or openings in the plate covering the tip (appearing as darker spots in the photograph). This structure is like that in *Diacanthaspis* described above, and whether or not hairs emerged from the tips of these spines is uncertain.

Subgenus CERATOCEPHALINA Whittington, n.subgen.

Type Species: *Ceratocephala (Ceratocephalina) tridens*
Whittington, n.subgen., n.sp.

Discussion: *C. (Ceratocephalina) tridens* displays many of the exoskeletal characters of *Ceratocephala* — the subtrapezoidal outline of the convex cephalon, broad, long (sag.) occipital ring, large basal, smaller second, and extremely small third lateral glabellar lobes, prominent eye ridge and eye lobe, and librigenal spine originating on the postero-lateral border of the free cheek; the thoracic pleurae are not furrowed and bear two pleural spines, the anterior shorter, with lateral barbs; the pygidium is short, triangular; paired axial spines are prominent on each segment, and the ornament is of large, well-spaced spines. Yet it is distinguished from any of the three species of *Ceratocephala*

in the Middle Ordovician of Virginia (and other species of this genus) by a well-marked group of characters: (1) the lesser inflation of the lobes (fronto-median and lateral) of the glabella: (2) the position of the large eye lobe, far back opposite the midpoint of the basal glabellar lobe, and the consequent alignment of the branches of the dorsal suture; (3) the prominent median occipital spine, as large as the paired spines; (4) the relatively longer pygidium, axis well-marked, and lacking the median border spine. The differences between *C. laciniata*, *C. triacanthais* (Whittington and Evitt, 1954) and *C. rarispina* n.sp., seem to be less than those between any one of them and *C. (C.) tridens*, and I have recognized these differences as of subgeneric rank. If the hypostome associated with *C. (C.) tridens* is correctly placed, the subsquare outline and well-defined subtriangular anterior lobe of the middle body afford further distinguishing characters of the subgenus.

Only the cephalon is known of *Whittingtonia bispinosa*, from the Upper Ordovician of Eire and Sweden (Text-fig. 17). It is distinguished from *Ceratocephala* (*Ceratocephalina*) by the far more prominent median glabellar lobe, the relatively narrow basal glabellar lobe, the more anterior position of the eye lobe, lack of median occipital spine, and less prominent ornament. *Proceratocephala* (Whittington, 1956b), also an Upper Ordovician genus, has more inflated median and lateral glabellar lobes, lacks the median occipital spine and has the paired spines differently situated, has well-marked pleural furrows in the thoracic segments, and a pygidium with more prominent border spines.

CERATOCEPHALA (CERATOCEPHALINA) TRIDENS Whittington,
n.subgen., n.sp.
Plate 16.

Holotype: USNM 124699 (Pl. 16, figs. 1-3, 18), locality 4.

Other Material: Paratypes USNM 124700 a-c, all figured specimens in USNM.

Geological Horizon and Locality: lower Edinburg limestone, localities 3 and 4.

Description: Outline and form of cephalon shown in Plate 16, figures 1-7. Occipital ring set off from posterior border by

change in slope and backward curve of posterior margin, longest (sag.) medially; occipital furrow deep only behind basal lateral glabellar lobes. Lobes of glabella gently convex, separated from each other by broad, shallow furrows, only the inner parts of the first and second glabellar furrows relatively deeper, and the third furrow represented by a subcircular pit behind the eye ridge (Pl. 16, figs. 3, 6); third glabellar lobe extremely small. Change of slope only separates glabellar from anterior border, axial furrows shallow beside first glabellar lobes, elsewhere glabella merges into cheeks. Eye lobe large, subspherical, situated on highest point of cheek, and opposite a point on midline just in front of occipital furrow. Palpebral lobe vertical, anteriorly merging with eye ridge, which curves forward to join with most anterior part of glabella. Eye surface (Pl. 16, figs. 23, 24), with each facet convex externally, concave internally. Anterior branch of suture curves forward, diverging slightly from eye ridge, crosses anterior border furrow on low sutural ridge, and turns abruptly to run inward and downward across anterior slope of border to meet rostral suture at obtuse angle. Rostral suture runs along outer edge of narrow (sag. and exs.) anterior border. Posterior branch of suture (Pl. 16, fig. 18) runs down the vertical cheek, in a curve convex outwards, and across posterior border furrow and border. Two branches of suture are approximately aligned and thus do not make an angle at eye lobe. Free cheek (Pl. 16, figs. 23, 24) with broad border occupying almost half the width at the librigenal spine, shallow border furrow, midpart of border, between rolled margin and inner part, concave upward. Librigenal spine arising inside edge of border, base merging into border, the low swelling extending forward especially conspicuous. Interior view (Pl. 16, figs. 6, 9) shows doublure widest laterally, and ridges formed by deepest parts of occipital and glabellar furrows. Rostrum must be short (sag. and exs.) but broad (tr.). Hypostome tentatively placed here (Pl. 16, figs. 19-22) sub-square in outline, middle body convex, divided by shallow furrows into sub-triangular anterior lobe and crescentic posterior lobe, well-marked depression in antero-lateral corner. Lateral notch extremely shallow, shoulder small, pointed, posterior border wide (exs.) with median notch. Major cephalic spines are librigenal and paired

and median occipital spines. The next size, thorn-like, include those on the major spines, those projecting from edge of lateral border, paired spines of glabellar lobes, palpebral lobe, eye ridge, free cheek, etc. Fine granular ornament extends over dorsal surface between these spines.

Number of thoracic segments unknown. Axis broad, pleura relatively narrow (tr.). Construction of axial rings and pleurae like *Ceratocephala* (cf. Whittington and Evitt, 1954, Pl. 8, figs. 8, 10), but appendiferal pits shallower and anterior pleural spines curved, directed outward and downward, not steeply downward as in *C. laciniata* and *C. triacanthéis*. The posterior pleural spines are directed slightly upward and progressively more strongly backward, so that on a posterior thoracic segment (Pl. 16, fig. 12) they point almost directly back. The pair of spines on the axial ring are long and curve outwards. Thorn-like spines occur on them and on the pleural spines. Pygidium (Pl. 16, figs. 15-17) with axis undivided, but the two pairs of axial spines suggest it may be composed of at least two segments. Pleural regions without border, one major pair of spines arising behind axis on upper surface, directed backward and upward; doublure narrow with broader (sag.) "tongue" projecting toward axis. Many short spines on edge of border, smaller spines on pleural lobes.

Discussion: From locality 4, where most of the specimens of *C. (C.) tridens* have been found, comes a single small cranidium of the same general type, but displaying certain differences (Pl. 15, figs. 26, 27, 30). Most striking are the long curving pair of occipital spines, the bases closer together, and the small median occipital spine. The external surface is covered with tiny tubercles, and the spines in the row on the fixed cheek are longer than those of *C. (C.) tridens*. The different appearance of the external surface of this cranidium may be the result of preservation, but the difference in the occipital spines is suggestive of a specific difference. Perhaps this cranidium represents a second species of *Ceratocephala* (*Ceratocephalina*).

Genus *PROCERATOCEPHALA* Prantl and Přibyl, 1949

Synonym : *Drummuckaspis* Prantl and Přibyl, 1949

Type Species : *Acidaspis terribilis* Reed, 1914.

Discussion: The type species has been described in detail elsewhere (Whittington, 1956b), and is like *Ceratocephala*, but differs in the presence of long paired spines and lateral lobes on axial and occipital rings, possessing 9 thoracic segments with deep pleural furrows, and a pygidium with a long major and short median border spine. The cephalon displays some features recalling *Miraspis*, but is too poorly known to allow detailed distinctions to be made. *P. terribilis* is known only from the Upper Ordovician of Scotland.

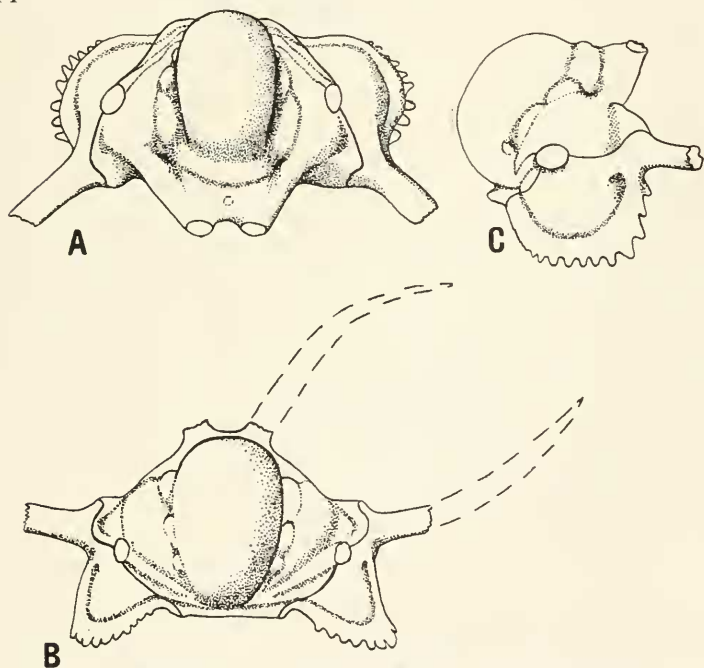


Figure 17. *Whittingtonia bispinosa* (M'Coy), Upper Ordovician, Chair of Kildare, Eire. A, B, C, incomplete cephalon, exterior, anterior, and left lateral views, approximately X 3. Drawn from originals of Whittington 1956b, Plate 59, figures 4, 5, 7, 8.

Genus WHITTINGTONIA Prantl and Přibyl, 1949
Text-figure 17.

Type Species: *Acidaspis bispinosus* M'Coy, 1846.

Discussion: Only the cephalon is known, and a well-preserved specimen has recently been described (Whittington, 1956b). It is distinguished from *Ceratocephala* by the three narrow (tr.) pairs of lateral lobes and wide (tr.), strongly convex fronto-median lobe which overhangs the anterior border and has a convex band across the base, and the short, thick spines on the lateral cephalic border. Specimens are known from the Upper Ordovician of Eire and Sweden.

Genus DICRANURUS Conrad, 1841

Text-figure 18.

Type Species: *Acidaspis hamata* Hall, 1859 (Whittington, 1956b).

Diagnosis: Occipital ring without posterior band, paired spines thick and long, recurved in a hook extending over the thorax. Small third lateral glabellar lobes. Eye lobe situated opposite basal glabellar lobe on highest part of convex cheek. No spines on lateral cephalic border. Nine thoracic segments; anterior pleural spine blade-like, with lateral barbs, curved downward and backward; convex posterior pleural band continued into stout posterior pleural spine, anterior directed outward, remainder outward and backward. Pygidium with pair major border spines only, connected by strong pleural ridge to first axial ring.

Geological Range: Lower to Middle Devonian.

Notes on Other Miraspinid Genera

Selenopeltoides Prantl and Přibyl, 1949, type species by original designation *Acidaspis hawlei* Barrande, 1852, from the

Figure 18. *Dicranurus monstrosus* (Barrande), Prokop limestones, ga₂. Middle Devonian, Lochkov, Bohemia. A, anterior view of cephalon, B, C, dorsal and right lateral views of entire exoskeleton, approximately X 1½. After Whittington 1956b, text-figure 4.

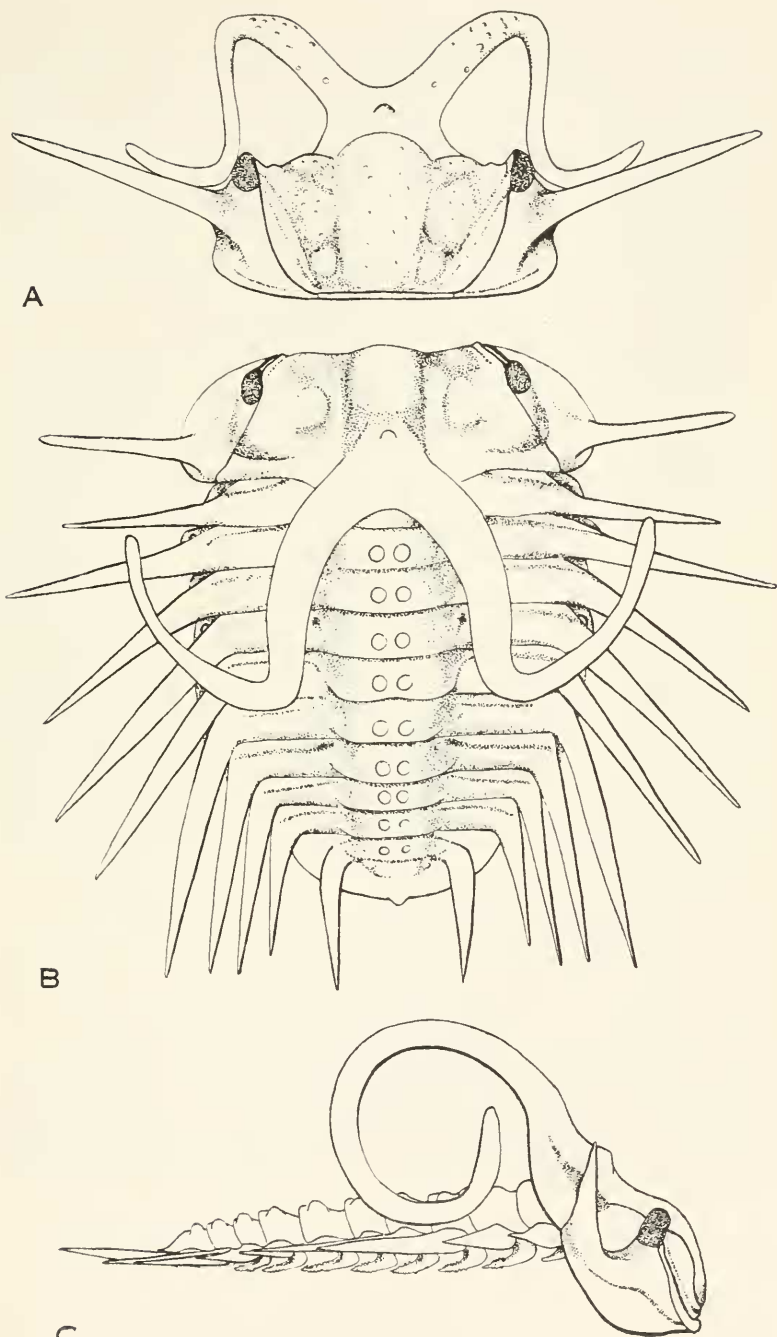


Figure 18

upper Middle Silurian of Bohemia. No material other than the original incomplete holotype (and an isolated pygidium, now missing) is known, so that the basis for a genus is most unsatisfactory. Erben (1952b) suggested that the type species was most closely related to *Dicranurus*, which appears probable.

Orphanaspis Prantl and Přibyl, 1949, type species by original designation *Trilobites orphanus* Barrande, 1852, Middle Silurian. Beside the type species, two others have been recognized in the Lower and early Middle Devonian of Germany (Erben, 1952a, pp. 306-308, 314-316, text-figs. 52, 54, Pl. 20, figs. 7, 13; 1952b), but all are based on pygidia only, of miraspinid type.

Koněprusia Prantl and Přibyl, 1949, type species by original designation *Acidaspis fuscina* Novák, 1883, lower Middle Devonian. Three species originally described by Barrande were placed in this genus by Prantl and Přibyl (1949, pp. 199-202), but of neither the type species nor these other species was new material described or new figures given. The pygidium of the type species is distinctive, the border spines being only one stout pair and a median posterior, but the cephalon is poorly known. Tentatively this material may be recognized as representing a separate genus, presumably of miraspinid type, but until it is better known its position will remain uncertain.

Ceratonurus Prantl and Přibyl, 1949, type species by original designation *Acidaspis krejčí* Novák, 1883. I have no new observations to add to those of recent authors (Prantl and Přibyl, 1949, pp. 189-192; Erben, 1952a, pp. 308-313; Erben 1952b), and all are agreed that this Lower and Middle Devonian genus is of *Ceratocephala* type. It may be derived from this latter genus or from *Miraspis*.

?Subfamily MIRASPINAE R. and E. Richter

ODONTOPLEURID PROTASPID

Plate 21, figures 23, 24.

Material: USNM, one incomplete specimen from locality 4.

Discussion: This specimen is smaller than either of the protaspides of *Diacanthaspis lepidus* n.sp. (Pl. 4, figs. 1-5) and *D. secretus* n.sp. (Pl. 6, figs. 1-5) from the same locality, but is of extremely similar form. It differs principally in that the fixi-

genal spine and those on the external surface are slimmer and less swollen at the base. On the parallel-sided glabella only the thick median occipital and axial spine pair 3 are present. On the cheek, which is most convex in the inner part, the fixigenal and spines A_1 , A_2 , A_3 , B, C (directed almost straight outward and somewhat upward), D (about midway between C and palpebral lobe), Pl and Er may be seen, and there is an additional spine about midway between A_2 and B. The protopygidium has a markedly triangular outline, convex axis bearing two pairs of spines, two pairs of spines on borders, at base of anterior of which is short upwardly-directed spine.

The presence of only spine pair 3 on the glabella and the outline of the protopygidium, as well as the slimmer spines on the external surface, make it unlikely that this protaspis is that of *D. lepidus* or *D. secretus*. The Stage 0 cranidium of *D. ulrichi* n.sp. (Pl. 8, fig. 10), has stout fixigenal and median occipital spines, but others are faint, and the outline also is unlike that of the cranidium of this protaspis. The Stage 0 cranidium of *Apianurus barbatus* n.gen., n.sp. (Pl. 19, fig. 2), has stouter spines, including paired occipital, pairs 2 and 4, and those of the anterior border, all of which distinguish it. Thus I am driven to suggest that this protaspis might be that of *Ceratocephala laciniata*, which is fairly abundant at this locality, but cannot exclude the possibility that it is that of the rare *C. (Ceratocephalina) tridens*, n.subgen., n.sp. No evidence can be offered for or against this latter possibility, since tiny cranidia of *C. (C.) tridens* are not known. The smallest known cranidia of *C. laciniata* (Pl. 14, figs. 2, 3) have an outline like that of the protaspis, notably the curve of the lateral sutural margin, anterior border without spines, eye lobe far forward, fixed cheeks lacking fixigenal spine but having all lettered spines and some additional. The glabella of these small *C. laciniata* cranidia, however, is strongly convex, spine pair 3 most prominent, but long, curved paired occipital spines are present as well as pairs 2 and 4, and the median occipital spine is small. It is chiefly this difference in the glabellae that makes me hesitate to identify this protaspis as that of *C. laciniata*, though there are also differences in the disposition of the lettered spines on the fixed cheek. Only the discovery of cranidia intermediate between this

protaspis and the smallest of *C. laciniata* would show how, if they belong to the same species, the transition takes place.

Subfamily APIANURINAE Whittington, n.subfam.

Diagnosis: Glabella narrows forward, occipital ring long (sag.), convex, long paired spines and median tubercle; well defined, parallel-sided median lobe, two pairs of lateral lobes fused. Eye lobe situated far back and about midway across cheek, two branches of suture forming a straight line inclined inward and forward to the sagittal line, free cheek narrow, librigenal spine arising about midway along lateral border and curving back. Hypostome shield-shaped. middle furrow arises at antero-lateral corner of middle body and runs inward and backward; small, pointed shoulders and shallow lateral notch. Thorax of unknown number of segments, pleurae convex (exs.), single large pleural spine. Pygidium with paired border spines, unpaired median border spine may be present, long major spine upwardly directed.

Geological Range: Middle to Upper Ordovician.

Genus APIANURUS Whittington, n.gen.

Type Species: *Apianurus barbatus* Whittington, n.gen., n.sp.

Diagnosis: Long occipital spines diverge at 60-80°; fused lateral lobes kidney-shaped. Large eye lobe opposite basal glabellar lobe. Hypostome widest anteriorly, convex middle body divided into triangular anterior and crescentic posterior lobe; small anterior, tiny posterior, wings. Pygidium with six or seven pairs border spines, flat pleural region bearing centrally-situated upright major spine. Long spines (except occipital) with thorn-like lateral spines, remainder of exoskeleton tuberculate or spinose.

Geological Range: Middle and Upper Ordovician. An incomplete cranidium and fragmentary free cheeks and thoracic segments testify to the presence of a species of this genus in the Lincolnshire limestone, below the Edinburg limestone.

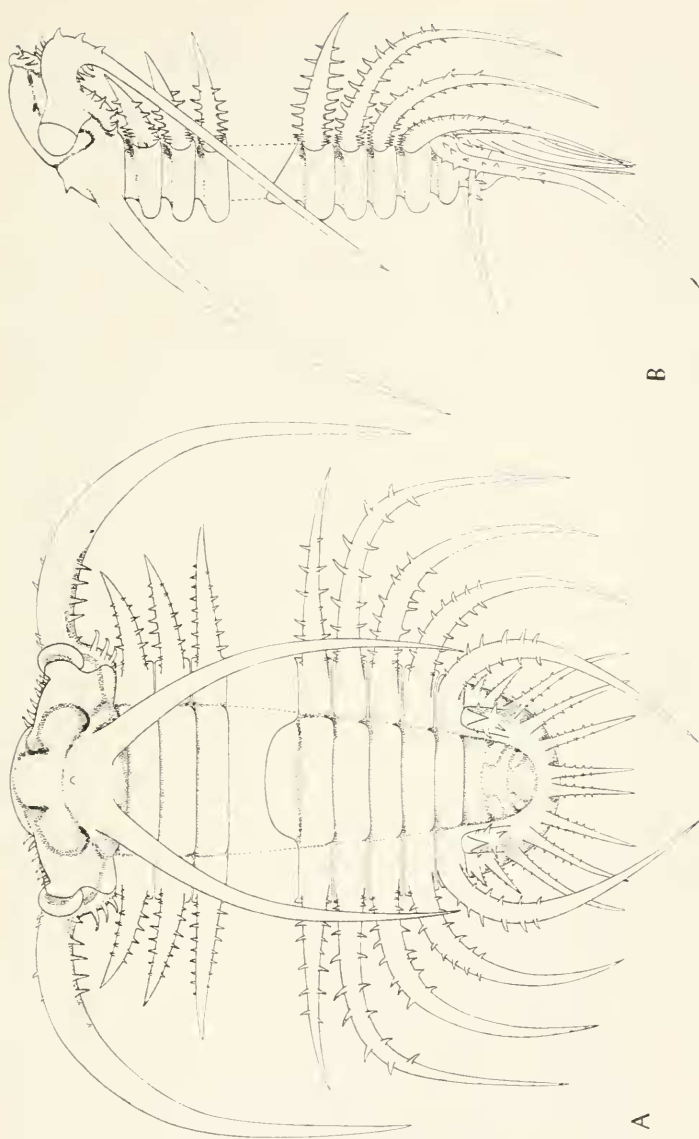


Figure 19. *Apianurus barbatus* n. gen., n. sp. Reconstruction, A, dorsal, B, right lateral views. Number of thoracic segments unknown. Approximately X 4.

APIANURUS BARBATUS Whittington, n.gen., n.sp.

Plates 17-19; 20, figures 1-17. 19: Text-figures 19-22

Holotype: USNM 124701 (Pl. 17, figs. 3, 4, 6), locality 2.*Other Material*: Paratypes, USNM 124702 a-e; all figured specimens in USNM.*Geological Horizon and Localities*: Edinburg limestone, localities 2, 3, 4, 6, 8.

Description: Cephalon moderately convex, outline in dorsal and anterior aspect elliptical. Glabella moderately convex transversely, gently convex longitudinally, maximum width across occipital ring, narrowing forward to half this width at anterior margin; length about two-thirds maximum width. Occipital ring of length (sag.) in dorsal aspect half that of rest of glabella, becoming narrower (exs.) laterally, outline of posterior margin a curve strongly convex posteriorly, outline of anterior margin a curve more gently convex anteriorly. Stout occipital spines diverge at about 60° and curve upward and backward, extending to a length three times the sagittal length of the cephalon. Small median occipital spine just behind occipital furrow. Latter shallow medially, deep behind basal lateral lobes. First and second glabellar lobes fused to give a kidney shape, the second the smaller, the first glabellar furrow represented by a subcircular pit adjacent to the median lobe. A pit anterior to the second glabellar lobe represents the second glabellar furrow, and is bounded anteriorly by the eye ridge as it fuses with the frontal glabellar lobe. Outline of anterior margin of latter curve convex forward, and separated by change of slope from narrow anterior border. Fronto-median lobe gently convex, change of slope separating it from lateral lobes, faint additional swelling running transversely across it between first glabellar lobes. Axial furrow not deep, but a narrow, unornamented band, marking reversal of slope between cheek and glabella. Cheek semi-circular in outline, maximum width opposite second glabellar lobe, rising steeply to large eye lobe. Transverse line through mid-point of eye lobe passes through mid-point of first glabellar lobe and runs just in front of occipital furrow. Anterior branch of facial suture runs straight forward and inward at about 45° to the midline, curving inward a little more as it

crosses the border on a sutural ridge. Posterior branch runs out and back in line with anterior branch for a short way, then curves in over posterior border. Latter longest (exs.) at suture, convex, and becomes shorter inward. Thus the occipital ring merges with inner corner of cheek rather than with posterior border. Fixed cheek slopes vertically behind eye lobe. Palpebral lobe with rim becoming well-defined anteriorly, and passing into broad, convex eye-ridge. Latter runs with a slight curve inward and forward to merge with frontal glabellar lobe. Eye surface almost hemispherical, external surface (Pl. 17, fig. 21) showing faintly the tiny facets. Lateral cephalic border rolled, shallow border furrow interrupted at about mid-length by swelling at the base of librigenal spine. Latter directed outward and slightly forward at first, then curving and slimming to point backward, and reach to a length about three times that of the cephalon (sag.). Just outside anterior branch of suture is antennular notch (Pl. 17, fig. 5), with a sharp projection at outer margin. Anterior border between sutures narrow (sag. and exs.), rostral suture running along outer edge. Rostrum unknown, but presumably wide (tr.) and short, sloping downward and inward. Doublure narrow on free cheek, absent on posterior border of cranidium, articulating half-ring long (sag.). On inner surface of cranidium (Pl. 17, fig. 12) outer part of occipital ring, first and second glabellar furrows make rounded projections but are not extended as appendifers. Width of hypostome (Pl. 18, figs. 1-5) at anterior margin greater than length, rounded postero-lateral outline, faint median posterior notch. Anterior wing small, tip rounded, no wing process. Lateral border narrow, gently convex, deep border furrow, shallow lateral notch and sharply-pointed shoulder. Posterior border wider and in median portion separated by shallow depression from median body. Outermost part of posterior border bent up sharply near mid-line. From the broad depression at antero-lateral corner the middle furrow runs straight inward and backward to define triangular, convex anterior lobe of the middle body. Posterior lobe crescentic in outline, inflated. Doublure of hypostome widest laterally, disappearing at anterior wing and pressed close to median part of posterior border so that edge is sharp. Ridge crosses doublure from point of shoulder to inner edge, immediately behind ridge doublure extended inward to form small tri-

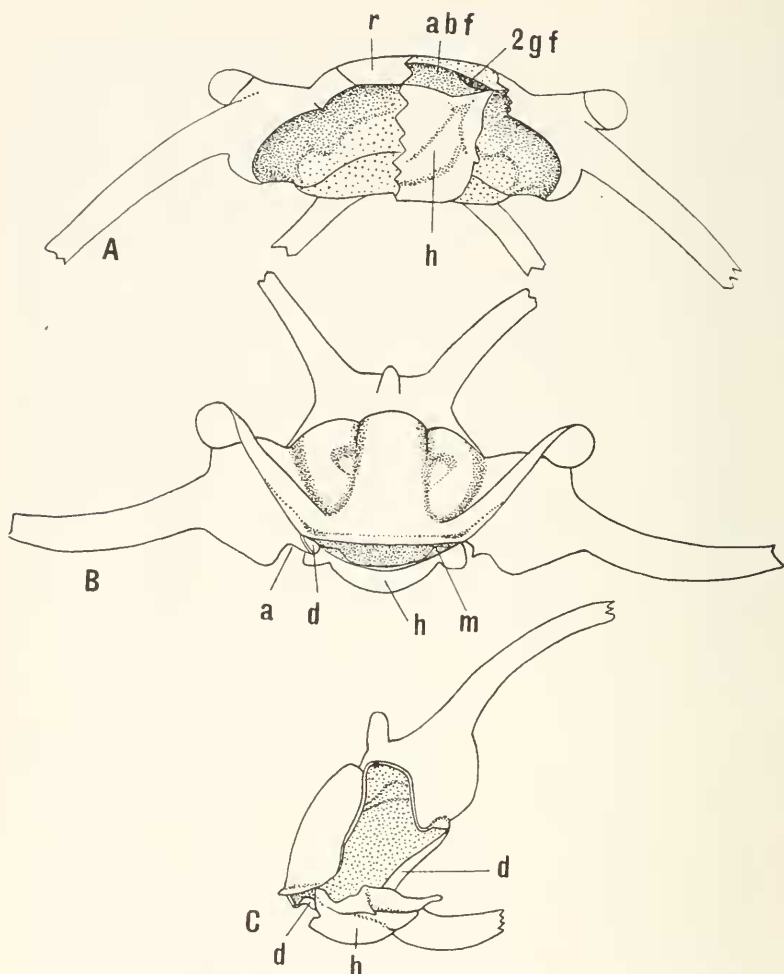


Figure 20. *Apianurus barbatus* n.gen., n.sp. Outline reconstructions of cephalon, approximately X 10. A, ventral view, right half of rostrum and left half of hypostome shown, anterior portion of left free cheek incomplete. B, anterior view, rostrum not shown and anterior portion of left free cheek incomplete. C, left lateral view, rostrum and left free cheek not shown. a, antennular notch; abf, ridge on inner surface corresponding to anterior border furrow; d, doublure of right free cheek; 2gf, ridge on inner surface corresponding to second glabellar furrow; h, hypostome; m, boss corresponding to depression at outer end of middle furrow; r, rostrum.

angular posterior wing. Perforation through doublure posterior to ridge (Pl. 17, fig. 19).

By mounting a cranium and free cheek of appropriate size in juxtaposition, as shown in Plate 17, figures 5, 7, 9-11, the approximate position and attitude of the hypostome has been determined (Text-fig. 20). The gently-curved hypostomal suture (Pl. 18, figs. 1, 5) fits against the rostrum, and the anterior wing is directed upward and outward, the tip lying beneath the deepened outer part of the anterior border furrow where it meets the furrow bounding the outer side of the eye ridge. There may have been muscles linking the wing and inner side of the furrow, but there is no wing process or socket. The depression at the outer end of the middle furrow forms a considerable projection on the inner surface (Pl. 18, fig. 2), and may have been a point of muscle attachment. Perhaps it was linked by muscles to the outer end of the anterior border furrow. The shape of the rostrum is suggested, and is consistent with the form of the few odontopleurid rostra known (Whittington, 1956b, Pl. 58, fig. 7; Pl. 59, fig. 3). If the cephalon rests on a flat surface on the antero-lateral cephalic border and librigenal spines, as portrayed in Text-figure 20 B, C, the middle body of the horizontal hypostome would lie on this surface.

Ornament of cephalon of close-spaced spines which curve characteristically toward the closed tip (Pl. 17, fig. 21; Pl. 18, fig. 22). The spines vary in size, the exoskeleton between their bases smooth, as are also the axial, occipital, and glabellar furrows. Arrangement of spines not perfectly regular, but symmetrical pairs of larger spines may be distinguished even on largest crania, on the occipital ring, median and lateral glabellar lobes, eye ridge, etc. (Pl. 17, fig. 2). Single row of symmetrical spines on anterior border of cranium. Large, curved spines are also regularly arranged on the border of the free cheek and the proximal portion of the librigenal spine (Pl. 17, figs. 1, 7, 14, 15) — e.g. four long and one short spine on the border behind the librigenal spine; stout spine at edge of antennular notch, one of same size midway to base of librigenal spine; 6 spines along outer side of proximal part of librigenal spine, etc. The characteristic curved spines are not present on the distal part of the librigenal spine, nor on the occipital spines. Much shorter, blunt,

spines are present, directed outwards on the proximal portion of the spine, but distally inclining more and more in the direction of the main spine, so that at the tip they lie at a low angle to the surface (Pl. 17, fig. 3). Toward the tip of the main spine, on the distal side of the base of the small spine, a minute opening is sometimes seen — apparently the locus of a sensory hair. Other cephalic spines do not seem to show such openings. Proximally, in the region where there are the large lateral spines, the under side of the librigenal spine is smooth, as is the doublure of the free cheek. The characteristic curved spines occur on the lateral and posterolateral borders of the hypostome (Pl. 18, fig. 1), but are reduced to granules on the posterior border. Similar spines are scattered on the lateral areas of the middle body, but the central portion is smooth.

Number of thoracic segments unknown. A sufficient number of the delicate segments are preserved to permit the reconstruction (Text-fig. 19 A, B), which is based on the assumption of a total of ten. Axis broad, two-thirds total width (excluding pleural spines) at anterior segment (Pl. 18, fig. 6), narrowing back to half its width at posterior segment (Pl. 18, fig. 9). Axial ring moderately convex, posterior margin forms a curve, convex posteriorly. Articulating furrow more strongly curved in same sense, outermost part deepened. Articulating half-ring longer (sag.) than axial ring. Pleura narrowest (tr.) in anterior segments, horizontally extended, without pleural furrow. Narrow (exs.) flanges developed, outer surface of each flat and inward and downward sloping. Ring and axial articulating sockets and processes scarcely at all developed, but lateral margin of pleura rolled under and fulcral socket and process prominent. Base of pleural spine swells out from upper, outer surface of pleura. Length, curvature and direction of pleural spines indicated in reconstruction. The characteristic curved ornamental spines are close together on the axial ring, varying in size, some larger ones paired. Similar spines more widely scattered on pleurae. Pleural spines ornamented like librigenal, with row of lateral, curving hooks on each side of proximal part, and the tiny inclined spines distally (Pl. 18, fig. 9). Similar openings to those on the tips of the occipital and librigenal spines seem to be present.

Pygidium (Pl. 18, figs. 11-13) semi-oval in outline, length

(sag.) a little more than one-third width at anterior margin. Axis moderately convex, a little wider than long, rounded posteriorly, rising from the flat pleural regions and not defined by deep furrows. Articulating furrow and half-ring like those of segments. First ring furrow broad and deep, curving forward to midline, extremities widened and deepened. Second ring

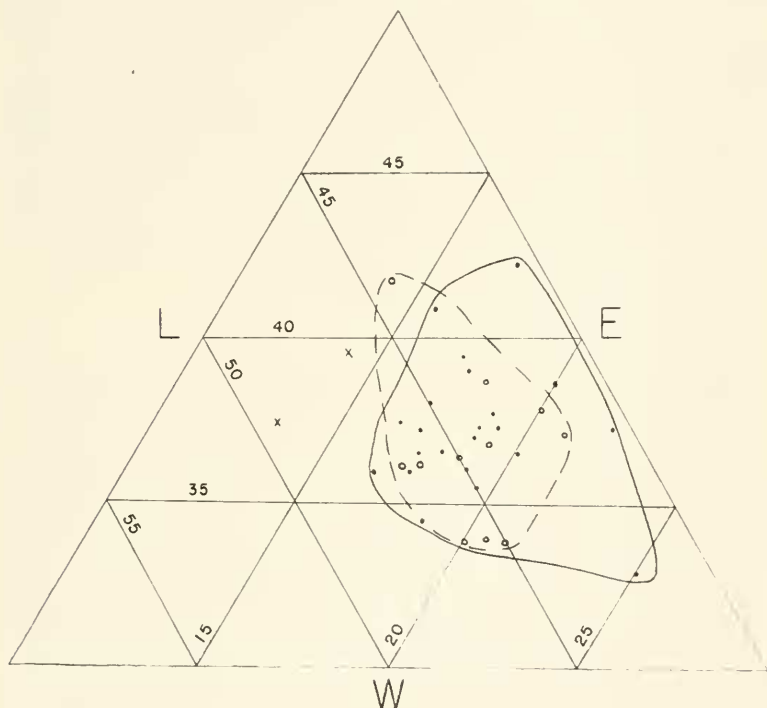


Figure 21. Triangular graph comparing relative proportions of dimensions of crania of *Apianurus barbatus* n.gen., n.sp. Those from the lower Edinburg formation, localities 2, 3, shown by dots enclosed by solid line. Crania from the Oranda formation, locality 8, shown by open circles enclosed by broken line. Two tiny crania from locality 3 shown by X (originals of Plate 19, figures 2, 9). L, sagittal length of cranium. W, width between spines B on posterior border. E, length (exs.) from anterior margin to midpoint of palpebral lobe. Measurements were made in exterior view, i.e. with isolated cranium resting on a horizontal surface.

furrow represented only by pair of oval, unornamented areas on terminal part of axis, corresponding in position to wider outer part of first furrow. In many specimens these two pairs of oval areas are translucent, the quartz much thinner over them, or broken, indicating that they may be areas of muscle attachment (cf. Whittington and Evitt, 1954, pp. 24-25). Long spine rises vertically from flat pleural region, opposite first ring furrow, and distally curves a little backward. Border of pleural regions with 6 pairs of spines directed outward and slightly upward, first pair short, second longer, third longest, and remaining pairs shorter inwards. Doublure of pygidium narrow, rolled under at antero-lateral corner forming articulating process. Ornament of curved spines on pygidium (Pl. 18, figs. 12, 13, 19) disposed as on thorax — dense, varying in size, and with some conspicuous pairs on the axis, more widely spaced on pleural regions. Upright and border spines with lateral barbs, and towards tips the tiny inclined spines are present, and the openings may be present.

Discussion: In addition to the material from the lower Edinburg formation (localities 2, 3, 4; Pls. 17-19), that from the Oranda formation (locality 8; Pl. 20, figs. 1-17, 19) also represents *Apianurus barbatus*. Comparison of parts of the exoskeletons from all localities reveals no consistent differences between them. Measurements of length and width of cranidia and of position of palpebral lobe in specimens from both horizons fall within almost the same area of a triangular graph (Text-fig. 21). Locality 8 in the Oranda formation is some $450 \pm$ feet higher in the section than localities 2-4 in the lower Edinburg, so that *A. barbatus* evidently has a long range in time. A few specimens (see Table 4) are known from locality 6, at an intermediate point in the section.

Figure 22. *Apianurus barbatus*, n.gen., n. sp. A, Stage 0 exoskeleton, dorsal view, drawn from originals of Plate 19, figures 1, 2, 5. Approximately X 32. B, cranidium, exterior view, drawn from original of Plate 19, figure 9. Approximately X 32. C, cranidium and right free cheek, exterior view, drawn from originals of Plate 19, figures 7, 8. Approximately X 32. D, cranidium and right free cheek, exterior view, free cheek from original of Plate 19, figure 11. Approximately X 32. E, cranidium, exterior view. Approximately X 32. F, cranidium, exterior view. Approximately X 16.

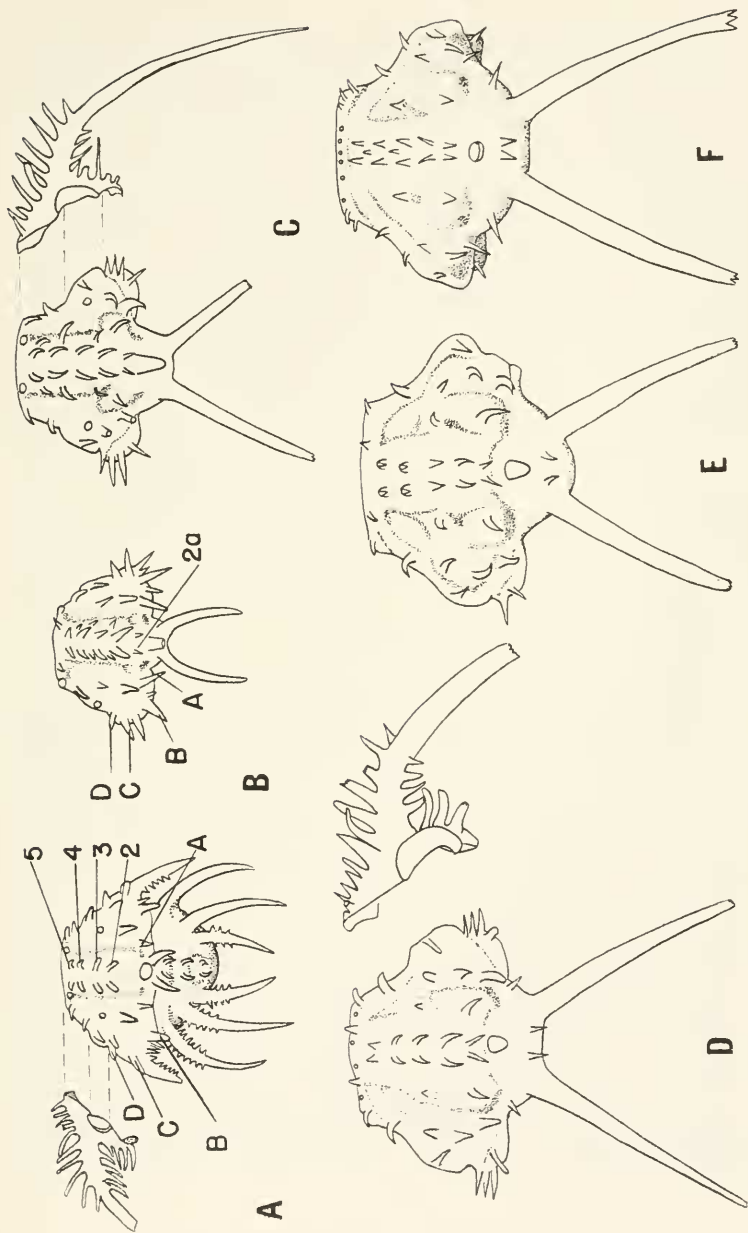


Figure 22

Development. Stage 0: Protaspis unknown, but the smallest known cranium, free cheek and pygidium from localities 3 and 4 (Pl. 19, figs. 1, 2, 5) have been associated (by analogy with *Diacanthaspis*) to show the probable nature of the Stage 0 exoskeleton (Text-fig. 22A). Outline of cranium (length (sag.) 0.41 mm.) trapezoidal, gently convex longitudinally, more gently transversely. Glabella outlined by broad, straight, axial furrows, short (sag. and exs.) occipital ring with prominent median and short curved pair spines, occipital furrow defined only distally, remainder of glabella without furrows, four prominent pairs short, curved, axial spines (2-5 in Text-fig. 22A). Narrow anterior border, fixed cheeks gently convex, palpebral lobes at two-fifths cranial length (exs.) from anterior margin. Posterior margin of fixed cheek runs directly outward from the axial furrow, and just beyond half the width bends abruptly to run outward and forward to the base of the long fixigenal spine. On the outer, postero-lateral area of the fixed cheek there are 4 paired spines (A, B, C, D in Text-fig. 22A), and tiny spines along the inner side of the fixigenal spine and adjacent outer part of the fixed cheek. Certain specimens (Pl. 19, figs. 4, 6) have the fixigenal spine retained on one side only. Their significance is discussed under "Ontogeny" in Part I. Free cheek of appropriate size to fit this smallest cranium (Pl. 19, figs. 1, 3; Text-fig. 22A) narrow, large eye surface situated at half length, big librigenal spine curving outward and backward. Anterior branch of the suture straight, posterior runs in curve convex outward, doublure projecting inward and fitting against doublure at base of fixigenal spine. Notch in anterior border outside suture very small. Long spines arranged in a constant pattern along outer edge of border and proximal edges of librigenal spine — conspicuous is variation in size of those along antero-lateral edge, curved spine at anterior basal edge of librigenal spine, numbers, curvature and/or inclination of remainder. Transitory pygidium of width at anterior margin 0.51 mm., length (sag.) 0.30 mm. Prominent axis bearing three pairs of curved spines, first two rings distinct, tip indistinct where posterior part of pygidium is bent sharply down. Pleural regions flat, borders bent down, 3 border spines arise on dorsal surface inside border, curving outward and backward. Doublure rolled under. Small barbs along sides of these border spines.

Further development of cephalon: Next largest crania (Pl. 19, figs. 9, 10; Text-fig. 22B) from localities 3 and 4 only. Parallel-sided glabella more convex, defined by deep axial furrows, tiny fifth pair of axial spines (2a in Text-fig. 22B) present just in front of occipital furrow. Small lateral pairs of spines also present outside pairs 2, 3, and 4. Extremity of occipital furrow a shallow pit, in front of which is small swelling representing the beginning of basal glabellar lobe. Large palpebral lobe situated at about the same position. Most striking is the absence of fixigenal spine and rounded outline of genal angle of fixed cheek. Paired spines A, B, C and D (Text-fig. 22B) are developed as in the smaller cranium, and there are one or two additional spines at the genal angle between B and C, as well as a small one on the fixed cheek between A and B. Free cheek associated with this size of cranium very like that of Stage 0, but has eye surface situated behind mid-length, posterior branch of suture running in curve convex outward and seemingly little or not at all modified despite absence of fixigenal spine. Notch in anterior border is wider, spines along margins and proximal part of librigenal spine similar in size and arrangement to those on the smaller cheek.

The next largest cephalon (Pl. 19, figs. 7, 8; Text-fig. 22C) show a marked increase in convexity of glabella and cheeks and in height of eye lobes. Occipital ring projects back farther behind cheeks, and paired spines now reach back to a length equal to that of cranium. Midpoint of eye lobes is at about half the length, cheeks slope steeply behind them to border furrow, which runs out to margin between spines A and B. Eye ridge faintly defined. Median occipital and five paired spines of glabella prominent, additional lateral pairs developed, including 2 pairs (one central and one just in front) on convex basal glabellar lobe. On cheek and borders main spines developed as before but additional pairs also present. Next largest cephalon (Pl. 19, figs. 11, 14-16; Text-fig. 22D) similar, eye lobes at about same position, eye ridge more clearly defined. Occipital ring with longer paired spines, and relatively reduced median spine. In front of pits at extremity of occipital furrow are convex, ovate, basal glabellar lobes. In front of these, in line with anterior part of eye lobe and at base of side of glabella, a prominent pair of

spines. In slightly larger cranidia (Pl. 19, figs. 18-20, 22, 23; Text-fig. 22E) the area around the base of these spines is slightly swollen, and represents the second glabellar lobes. A deep pit represents the first glabellar furrow, and a faint swelling outside it connects the two lobes. Thus the bean-shaped fused lateral lobes are present at this stage, and become more prominent as the cranidium increases in size, swelling up to partly fill the depression between eye lobes and glabella. Other changes as size increases include appearance of swelling on median glabellar lobe just in front of occipital furrow, backward movement of eye lobes with consequent steeper slope behind them, and increased prominence of eye ridges. Many more ornamental spines appear, mostly paired, and a median row on the median glabellar lobe. The relative size of these spines diminishes, but even in the largest cranidia (Pl. 17, figs. 2, 3) the numbered and lettered pairs may be recognized by their slightly larger size, and most spines retain the characteristic curve so prominent in tiny specimens. The chief change in the free cheek from the size shown in Text-figure 22A is the backward movement of the eye lobe, so that the postero-lateral slope behind it is steep or overhanging. The arrangement of the spines on the border and proximal part of the librigenal spine remains basically the same, though the curved spine at the anterior basal edge of the librigenal spine is reduced, and an additional large spine (making six in all) appears along the anterior proximal margin of the librigenal spine. The margin of the antennular notch remains smooth, but the outer edge bears a large spine. Because the broad, swollen base of the librigenal spine merges into the cheek a border becomes defined by a shallow border furrow only near the branches of the suture.

Smallest known hypostome (Pl. 19, figs. 12, 13) 0.4 mm. in length (sag.), 0.55 mm. in width across anterior wings, proportions of various parts similar to adult. There is little change with increasing size.

Thorax and pygidium. Next largest transitory pygidium (Pl. 19, fig. 24) to that assigned to Stage 0 (Pl. 19, fig. 5) has three pairs of spines on the axis, 3 pairs long border spines, with lateral barbs, similarly directed to those of the earlier stage. An upright spine at the base of the anterior two border spines. Larger transitory pygidia (Pl. 19, figs. 25, 27-29) have four

pairs axial spines and four pairs border spines, the fourth border pair short, blunt, situated at tip. Latter less steeply bent down. First three border spines with lateral barbs and upright spine at base, direction and curvature shows slight variation, perhaps associated with stage. Latest transitory pygidium (Pl. 19, fig. 26) of length (sag.) 0.36 mm., width 0.7 mm. with 4 pairs of axial spines, posterior two close together at termination. Long, curved spines arising from the antero-lateral portions of pleural regions are pleural spines of what is to become last thoracic segment. Bases of broken-off pair of upright spines on pleural regions are opposite 3rd and 4th axial spines. Four pairs of border spines, third pair larger than others. Posterior tip of this pygidium not bent down. Small true pygidium (Pl. 18, figs. 23, 24) has first axial ring defined, with its pair of axial spines, and posterior part of axis bears two pairs of axial spines (and presumably therefore includes at least 2 segments). Swollen base of upright spine on the pleural region is connected with first axial ring. Margin with tiny anterior pair of spines and 4 larger pairs, third of these distinctly longer. As size increases (Pl. 18, figs. 16-18, 20, 21) the adult appearance is attained, except that there are still only 5 pairs of marginal spines, the anterior short, the others becoming equal in size. There are three pairs of axial spines, and a median spine on the tip of the axis. Large pygidia (Pl. 18, figs. 11-13) have six pairs of marginal spines, the first much shorter and slimmer than the rest. Behind the ring furrow the axis includes two pairs of axial spines, and a median spine at the tip.

Specimens from Localities 2 and 3

Differing from *Apianurus barbatus* n.gen., n.sp.

Under this heading may be grouped the following:

(a) Cephalae and pygidia from both localities which are so strikingly different as to be regarded as representing a species of a distinct genus, described below as *Calipernurus insolitus* n. gen., n. sp.

(b) Cranidia from locality 2 which are like *A. barbatus* but are smoother — i.e. the spines are short, reduced to tubercles, or absent. These are described below as *A. glaber* n.sp.

(c) Pygidia occurring at both localities, distinguished from *A. barbatus* by being smoother and having shorter, inwardly-curved upright spines. These are here regarded as belonging with cranidia (b).

(d) A second type of pygidium occurring at locality 2, having the typical curved spine ornament of *A. barbatus*, but the upright spines are very short, and there are 7 pairs of spines on the border. This pygidium is described as *Apianurus* sp.ind.

(e) Three types of hypostome from locality 2, each different from that of *A. barbatus*. The one differing most has been assigned to *Calipernurus insolitus* n.gen., n.sp., the smooth one to *A. glaber* n.sp., the third described under "*Apianurus* sp.ind."

Each of the groups of specimens included under (a) to (e) is distinct, and there is no gradation between groups or between any one of them and *A. barbatus*. Within each group except (e) there are specimens of different sizes, showing that the distinctive characters of the group are not those of one particular size (i.e. growth stage). Table 4 shows the relative abundance of the different species at the different localities. Only *A. barbatus* is found in strata above the lower Edinburg. If the specimens grouped under (b), (c), and (d) were expressions of the morphological range of variation of *A. barbatus* one might expect them to be represented in the sample from locality 8. The fact that they are not suggests that they represent distinct species. This same pattern of distribution is displayed by species of other genera from localities 2 and 3, e.g. among the hundreds of specimens of *Dimeropyge virginensis* Whittington and Evitt (1954, pp. 37-42, Pl. 2, Pl. 3, figs. 1-30) are a small number that are distinctly different and do not grade morphologically into the common form, and which I regard as a separate species. One possible explanation of the "common" and "rare" species of the same genus at the same locality is that they represent sexually dimorphic forms of the same species, but this explanation can hardly be removed from the realm of speculation. In this connection Hintze (1953, p. 150) has discussed the occurrence of two pliomerid species at the same horizons of the Pogonip group, but in this case the two species are apparently equally abundant.

TABLE 4
Numbers of Exoskeletal Parts of all Sizes of *Apianurus* n.gen. and *Calipernurus* n.gen.

Locality	<i>Apianurus barbatus</i> n.gen., n.sp.			<i>Calipernurus insolitus</i> n.gen., n.sp.			<i>A. glaber</i> n.sp.			<i>A. sp. ind.</i>	
	Cranidia	Pygidia	Hypostomes	Cranidia	Pygidia	Hypostomes	Cranidia	Pygidia	Hypostomes	Pygidia	Hypostomes
2	115	82	15	21	17	2	13	20	5	12	4
3	95	58	17	12	6	0	0	9	0		
6	5	2	0								
8	28	56	28								

APIANURUS GLABER Whittington, n.sp.

Plate 21, figures 1-15.

Holotype: USNM 124703 (Pl. 21, figs. 1-3), locality 2.*Other Material*: Paratypes, USNM 124704a, b; other figured material in USNM.*Geological Horizon and Locality*: lower Edinburg limestone, localities 2, 3.*Description*: Cranium (Pl. 21, figs. 1-7, 11, 12) differs from that of *Apianurus barbatus* n.gen., n.sp. (Pl. 17, figs. 1-12) in that:

(1) Occipital ring with slightly depressed posterior band, widest (exs.) laterally, extremely narrow medially. In front of it a low ridge connects inner, posterior bases of occipital spines. Median occipital spine prominent, area between it and bases of occipital spines flattened, not evenly inflated. Paired occipital spines more divergent proximally, but curved so that distally they are directed slightly inward, not outward. Extremity of occipital furrow deeper, forming a more prominent projection on inner surface.

(2) Palpebral lobe less steeply inclined, eye ridge running forward and inward slightly farther out from lateral glabellar lobes, then curving more strongly in to meet frontal lobe of glabella. Anterior part of eye ridge less convex, and shallower depression outside it. Posterior border juts out slightly farther, and outer, sutural edge more acutely rounded.

(3) Larger crania with low tubercles on external surface, not curved spines. Tubercles are fewer in number than spines of *A. barbatus*, and on the glabella do not show any obvious paired arrangement. Lateral and postero-medial parts of occipital ring smooth. Smallest crania bear short spines on the glabella, few on occipital ring, but the fixed cheek bears spines with the characteristic *A. barbatus* curve, symmetrically arranged. These latter are reduced to rounded tubercles in the large crania, but retain the symmetrical arrangement.

A hypostome (Pl. 21, figs. 13, 14) from locality 2 differs slightly from that of *Apianurus barbatus* (Pl. 18, figs. 1-5), and is assigned to *A. glaber* principally because it is almost without ornament, there being only a few tubercles on the lateral border

adjacent to the shoulder. The outline is more rectangular, the median part of posterior margin being straight, the postero-lateral border broader. Middle furrow of middle body is distinct to midline, and does not fade out there, as in *A. barbatus*, and the same is true of the posterior border furrow.

Free cheek and thorax unknown. Pygidium attributed to this species (Pl. 21, figs. 8-10, 15) of the same form as that of *A. barbatus* (Pl. 18, figs. 11-13), with the same number of border spines but directed slightly more upward. Distinctive are the upright spines on pleural regions, short and inwardly curved, rather than long and curving back. Low tubercles on external surface, not short spines, a few on axial rings and scattered over pleural regions. Border and upright spines with lateral barbs. The reduction of the ornament on the axis reveals clearly the supposed areas of muscle attachment, over which the quartz is thinner. Three segments are distinct, the ring of the third outlined by an inverted V-shaped line of tubercles which enclose the tip of the axis. There is a median tubercle at the extreme tip, and between this and the ring of the third segment the quartz is also thin. This triangular area presumably represents the muscle attachments of a 4th segment.

APIANURUS Whittington sp.ind.

Plate 21, figures 16-22, 25, 26.

Material: Figured specimens USNM 124705a-e. lower Edinburg limestone, locality 2.

Description: Pygidium known only from locality 2 and differs from that of *Apianurus barbatus* n.gen., n.sp. (Pl. 18, figs. 11-13) in that the pleural regions are relatively wider, the upright spine small and short, and there are one short and six long pairs of border spines, longer and slimmer and slightly more upwardly directed. The ornament is of typical curved spines like those of *A. barbatus*, and there are lateral barbs on upright and border spines. The smallest specimen (Pl. 21, fig. 21) is 1.6 mm. in width at the anterior margin, and exhibits the same distinguishing characters, except that there are 1 short and 5 longer pairs of border spines. However, pygidia of *A. barbatus* of this size also have one less pair of border spines.

A few specimens of a hypostome (Pl. 21, figs. 20, 22, 25, 26), occurring at locality 2, differ from that of *Apianurus barbatus* (Pl. 18, figs. 1-5) in the following respects: (1) smooth even curve of outline of anterior margin without the projection in front of middle body; (2) smooth curve, rather than V-shape, made by confluent middle furrows; (3) posterior lobe of middle body evenly inflated, not divided by a flattening near the mid-line; (4) lateral notch less well defined, anterior edge merging with adjacent border.

Both these exoskeletal parts are distinct from corresponding parts of *Apianurus barbatus* and *A. glaber*, and seem to represent at least one additional species.

APIANURUS aff. FURCATA (Linnarsson, 1869)

Plate 20, figures 18, 20-25.

Material: PMO 66691a, incomplete cranidium; 66691b, small fragmentary cranidium; 66690, cranidium with incomplete occipital spines, all from Chasmops limestone, Guttormsberget; 3673, cranidium from Upper Chasmops limestone, Ferneholmen, Asker; 5647, pygidium from Bygdøy, near Oslo, Norway.

Geological Horizon: Chasmops limestone, middle Caradoc (Størmer, 1953, p. 130), or approximately late Black River or early Trenton (Twenhofel et al., 1954). The block from Bygdøy contains, besides the pygidium, cranidia and pygidia of "*Bronteopsis*" *gregaria* type (Cooper, 1953, Pl. 9) and *Remopleurides*, genera characteristic of the lower Edinburg of Virginia.

Description: Cranidium typical of the genus, differing from that of *Apianurus barbatus* n.gen., n.sp. (Pl. 17, figs. 2-12) principally in that: (1) occipital ring relatively a little longer and occipital spines more divergent; (2) fronto-median and fused lateral glabellar lobes less inflated; (3) palpebral lobe larger and less steeply sloping, and eye ridge just in front of lobe appears broader and more prominent. The tubercles of *A. aff. furcata* may be the bases of spines like those of *A. barbatus* n.gen., n.sp., and the number and distribution is similar.

The small pygidium (Pl. 20, fig. 20) is characteristic, having the large upright spine on the pleural region (broken off at the

base), and 6 pairs of border spines, the anterior pair small.

Discussion: The following species have been described from Sweden and the East Baltic:

Apianurus furcata (Linnarsson, 1869, p. 65, Pl. 1, fig. 18) cranidium from the Chasmops (=Beyrichia) limestone of Västergötland, Sweden.

Apianurus kuckersiana (Schmidt, 1885, pp. 4-5, Pl. 1, figs. 2, 3; Öpik, 1937, p. 47, Pl. 24, figs. 3, 4) from the Kukruse (C₂) stage of Estonia. Öpik figured the characteristic pygidium as well as the cranidium.

Apianurus kuckersiana var. *mickwitzii* (Schmidt, 1907, pp. 23-24, Pl. 1, fig. 19), cranidium from the Keila (D₂) stage of Estonia.

Apianurus asklundi (Thorslund, 1940, pp. 154-155, Pl. 6, fig. 14), cranidium from the lower Chasmops limestone, Jemtland, Sweden.

All are from the Chasmops limestone or its equivalents, and presumably closely related. I have not had an opportunity to examine the original material, and so cannot venture an opinion as to how many species are represented. I have used the oldest specific name for the Norwegian material, rather than create another name. It is notable that many of the genera of trilobites of the lower Chasmops limestone listed by Thorslund (1940, pp. 184-185) occur also in the Edinburg limestone — e.g. *Trinodus*, *Remopleurides*, "*Bronteopsis*" (= *Stygina*? of Thorslund, 1940, p. 137), illaenids, *Dimeropyge*, *Ampyx*, *Lonchodomas*, *Sphaerocrochus* (see Cooper, 1953; Whittington and Evitt, 1954).

Apianurus clevei (Warburg, 1925, pp. 243-245, Pl. 6, fig. 1), a cranidium from the Upper Ordovician Boda limestone of the Siljan district, central Sweden, appears to represent the youngest known species of *Apianurus*. Warburg also described a hypostome (1925, pp. 253-254, Pl. 6, fig. 7) and an incomplete pygidium (pp. 241-242, Pl. 6, fig. 9) from other localities in the Boda limestone which may well represent this same species.

Genus *CALIPERNURUS* Whittington, n.gen.

Type Species: *Calipernurus insolitus* Whittington n.gen., n.sp.

Diagnosis: Differs from *Apianurus* in that: (1) Cephalon is

relatively wider, six-sided rather than ovate in outline, and less deep; (2) occipital ring with lateral regions more sharply set off from swollen median portion, occipital spines diverge at 90° or more and directed close above thorax; (3) eye lobe farther for-

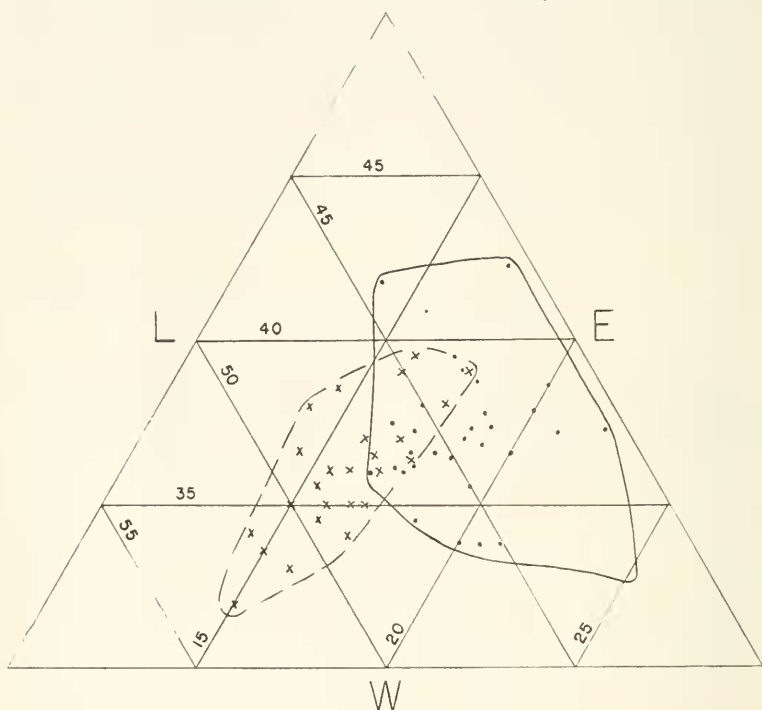


Figure 23. Triangular graph comparing relative dimensions of cranidia of *Apianurus barbatus* n.gen. n.sp. (shown by dots enclosed by solid line, the dot in the lower right-hand corner has been accidentally omitted — compare Text-fig. 21.) and *Calipernurus insolitus* n.gen., n.sp. (shown by crosses enclosed by broken line). L, sagittal length of cranium. W, width between spines B on posterior border. E, length (exs.) from anterior margin to midpoint of palpebral lobe. Measurements were made in exterior view, i.e. with isolated cranium resting on a horizontal surface.

ward, opposite first glabellar furrows; (4) pygidium with 4 lateral and one median border spine, posterior three of equal size, major spines on pleural regions directed backward and

slightly upward, curving inward in caliper-shape; (5) ornament of large tubercles rather than slim, thorn-like spines or small tubercles.

Geological Range: Middle Ordovician.

Discussion: Text-figure 23 illustrates the generally greater width of cranidia of *Calipernurus* compared to those of *Apianurus*, and the greater distance from the anterior margin back to the palpebral lobe in *Apianurus*.

At least four species of *Apianurus* are here recognized, from the Appalachian, Scandinavian and Baltic areas. All have the less divergent occipital spines, and the associated pygidium has pairs of border spines and the upright major spines. The *Calipernurus* type of cranidium and pygidium seems to be known only from Virginia, and is here regarded as representing a different but evidently closely allied group, of generic rank.

CALIPERNURUS INSOLITUS Whittington, n.gen., n.sp.

Plates 22-24; Text-figures 23, 24.

Holotype: USNM 124711 (Pl. 22, figs. 1-3, 6; Pl. 23, figs. 1, 3).

Locality 3.

Other Material: Paratypes, USNM 124712 a-d; all figured material in USNM.

Geological Horizon and Localities: Lower Edinburg limestone, localities 2, 3.

Description: Cephalon wider than long, outline (ignoring major spines) roughly six-sided; cranidium trapezoidal in outline, anterior margin less than half width of posterior. Glabella widest at occipital ring, occipital furrow shallow medially, outer part deep, diagonally directed outward and forward. Median part of occipital ring considerably higher than lateral, and bearing a short, stout median tubercle and the occipital spines; latter diverge at 90° or more (more in most larger specimens), proximal part straight and directed low over thorax, distal part curved inward and tapering. Fronto-median glabellar lobe subparallel-sided, gently convex posteriorly, moderately convex anteriorly, sloping steeply down to shallow preglabellar furrow. Portion between basal lateral lobes merges with these lobes, and is set off by faint transverse depression almost in line with pits representing basal glabellar furrows; greatest convexity of

fronto-median lobe in front of this depression. First and second glabellar lobes fused, kidney-shaped in outline and gently convex, separated by change in slope from fixed cheeks, posterior lobe slopes vertically to occipital furrow, second separated by sharp change in slope from median. First and second glabellar

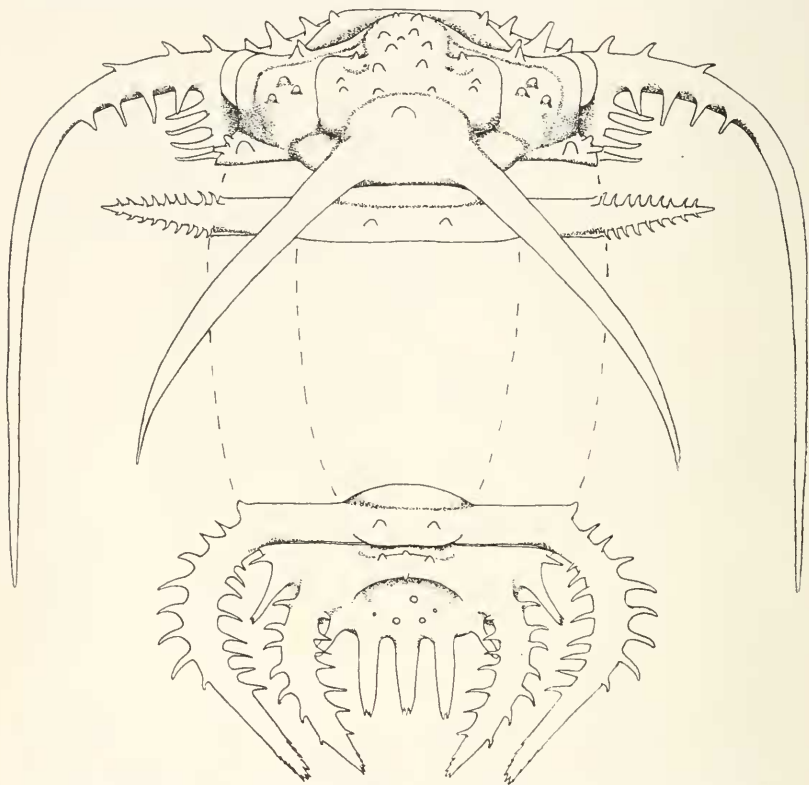


Figure 24. *Calipernurus insolitus* n.gen., n.sp. Reconstruction, dorsal view, number of thoracic segments unknown. Approximately X 10.

furrows represented by circular depressions, the first at the inner margin of the fused lateral lobes, the second at the inner, anterior corner of these lobes. Highest point of large eye lobe on transverse line passing just behind first glabellar furrows and level with crest of glabella in this line. Palpebral lobe slopes

steeply, broad rim passes into broad, convex eye ridge which runs straight inward at 45° , passes close to antero-lateral margin of fused lateral lobes and merges into frontal glabellar lobe. Eye surface hemispherical (Pl. 23, figs. 9, 10), outer surface almost smooth, facets faintly visible on inner surface. Anterior branch of suture runs on low sutural ridge straight forward and inward to anterior margin, where it meets rostral and connective suture. Posterior branch of suture runs back in line with anterior branch across border, then curves inward across doublure. Anterior border narrow (sag.) medially, becoming wider laterally and merging with sutural ridges. Deep depression parallels eye ridge on outer side, separating it from border and sutural ridge. Fixed cheek inside eye lobe slopes gently inward to margin of fused lateral glabellar lobes, inside and behind eye lobe it slopes steeply, almost vertically, down to occipital ring and posterior border furrow. Latter commences at lateral margin of occipital ring and runs forward and outward, so that convex border is widest at suture. Free cheek narrow, librigenal spine arises in front of eye lobe and curves outward and backward, the distal part directed straight back. Lateral border gently convex, defined by shallow border furrow, and runs from posterior branch suture to merge with swollen base of librigenal spine. No antero-lateral border is defined, though there is a depression between the sutural ridge and swollen base of the librigenal spine. Shallow antennal notch in vertical border of free cheek adjacent to anterior suture (Pl. 23, fig. 1). Doublure of free cheek widest behind notch, narrowing back and ending at posterior suture. Posterior border without doublure, articulating socket just inside suture. On inner surface of cranidium (Pl. 23, fig. 4) doublure of occipital ring and ridges, made by outer parts occipital furrow, are seen. First, and especially second glabellar furrows, and depression outside eye ridge, also project ventrally. Rostrum unknown, but evidently (Pl. 23, fig. 1) broad (tr.) and short (sag. and exs.), lateral margins converging backward, fitting so that outer surface faces almost directly downward. Two specimens only are known of the hypostome (Pl. 23, figs. 11-15). Anterior margin projects forward in front of convex middle body. Latter divided by shallow middle furrows which run inward and backward to about three-quarters

of the length and do not reach the midline. Posterior lobe crescentic, convex, especially toward the tips. Lateral borders horizontal, shallow border furrows, shallow lateral notch and sharply-pointed shoulder. Posterior border little wider than lateral, bent to slope steeply dorsally, border furrow shallow. Doublure widest at shoulder, where it is crossed by a sharp ridge, narrowest posteriorly. Tiny perforation just behind shoulder ridge (Pl. 23, fig. 15). The smaller specimen (Pl. 23, figs. 13, 14) has short, triangular anterior wings, but these are absent in the larger specimen (Pl. 23, figs. 11, 12, 15) and both antero-lateral corners are cut off. This truncation seems not to be accidental breakage, but is symmetrical. This hypostome differs from that of *Apianurus* (Pl. 18, figs. 1-5) in the much greater inflation of the middle body posteriorly, less distinct middle furrows, inclination of posterior border, smaller lateral notch, smaller opening in doublure, and ornament. It is accordingly regarded as probably belonging to *Calipernurus*.

External surface of cephalon with scattered tubercles, area between them, and all furrows, smooth. Largest is the median occipital tubercle, in the rounded top of which are four tiny depressions set at the corners of a square (Pl. 23, figs. 7, 8). Next largest in size are various symmetrically placed tubercles — pairs on the fronto-median and lateral glabellar lobes, pair at antero-lateral corners of cranidium, pair on outer edge of eyeridge at midlength, three just inside eye on fixed cheek, and one about at midpoint, one at extremity, of posterior border. Smaller tubercles are scattered, some symmetrically, on the cranidium and free cheeks, including base of librigenal spines. On the borders of the free cheek and proximal part of the librigenal spine are thorn-like spines, constant in number, position and direction. On the librigenal and occipital spines are short spines directed distally at a low angle to the axis of the spine, and becoming longer distally. There are openings at the base of these spines on the distal side (Pl. 23, fig. 6), but tubercles and spines elsewhere on the cranidium seem to be imperforate, and the bases of the tiny depressions in the occipital tubercle seem to be closed. Hypostome with tubercles on lateral borders only.

Few thoracic segments known, and number in thorax unknown; reconstruction (Text-fig. 24) assumes number was 10.

One segment from anterior part of thorax (Pl. 24, figs. 15, 16, 19) shows relatively wide, convex axis and horizontal, unfurrowed pleurae. Extremity of articulating furrow deep, articulating half ring as long (sag.) as axial. Pleural spines curving out and down, directed slightly forward. Doublure rolled under at base spine, and articulating process on anterior edge, socket on posterior edge. Smooth band runs across highest part of axial ring and pleurae into base pleural spine. Tubercles outside this band, some larger ones on posterior edge axial ring and on slope of articulating furrow paired. Lateral margins of pleural spine with row of close-spaced, curved spines. Two incomplete segments from the posterior part of the thorax, and an incomplete segment, possibly the posterior (Pl. 24, figs. 22, 23, 26), have the pleural spine curved like that of the major pygidial pleural spine. Smooth median band, and larger tubercles on posterior edge of axial ring and flanges of pleura are rounded like those of the cephalon, some on the axis paired. These segments are placed in *Calipernurus* because smooth band resembles that on occipital ring and posterior border (Pl. 23, fig. 5), deep extremities of articulating furrow resemble those of occipital furrow, and because pleural spines and bands on them are like those of major pleural spine of the pygidium.

Pygidium (Pl. 24, figs. 25, 27, 28) more than twice as wide as long, axis of same width as pleural region at anterior margin. First axial ring prominent, in front of it shallow articulating furrow and long (sag.) articulating half-ring. Posterior edge of axial ring descends vertically to gently convex posterior part of axis, which merges into pleural regions except antero-laterally, where shallow depressions occur. First axial ring connected across pleural lobes by low pleural ridge to base of major pleural spine, which arises inside margin and curves upward and inward. Rest of pleural regions flat, margin rolled, no border furrow. From vertical margin of border, four pairs and one median posterior spine arise—a pair of similar size flanking the median spine, a short pair just inside and beneath the major spine, and two pairs in front, the anterior tiny. Two specimens (Pl. 24, figs. 11, 18) lack the median border spine, and one (Pl. 24, fig. 17) has the median bifurcate at the tip, but lacks the pair flanking it. Such variation is unusual in this material.

Doublure sharply bent up, widest posteriorly, appendifers not developed, but areas of muscle attachment (shown by thinness of quartz) include extremities of articulating furrow, and corresponding areas behind first ring. In some species the entire area of the axis behind the ring is of thinner quartz, suggesting that it is all an area of muscle attachment. Ornament of rounded tubercles, paired and median on axial ring, pair at center of rest of axis, row of two or three at tip. Other tubercles on anterior region of pleural regions and base of major pleural spines. Latter with row of curved, thorn-like spines along lateral margins, also tubercles and distally-directed sharp tubercles, near tip. Latter have openings at base on distal side (Pl. 24, figs. 21, 24). Other border spines with short spines scattered on them, not in regular rows, directed distally at tips and with openings.

Development. Cranidium. Smallest known cranidium (Pl. 24, fig. 1) of length (sag.) 0.78 mm. Occipital spines diverging at about 90°. Glabella convex, parallel-sided, occipital ring prominent, with median tubercle and paired spines; fronto-median lobe with 5 pairs of axial spines — 2a, 2, 3, 4, and 5. Extra spine on left side between 3 and 4, median spine between 4 and 5. Median lobe between spines 2a and 2 with slight extra inflation. Basal glabellar lobe small, gently inflated ovate area low on side of fronto-median lobe, one median spine; second glabellar lobe smaller and fainter. Palpebral lobe situated in front of half length of cranidium, strongly raised, low eye ridge runs forward and inward. Narrow anterior border; posterior border widens (exs.) outward. Most prominent spines on fixed cheek include A₁, A₂, A₃, B, C, Pl, Er, and one of similar size at extremity of anterior border. Larger cranidium 1.08 mm. in length (sag.) (Pl. 24, figs. 5-7) has similar glabella, but the lateral lobes are larger, more inflated, separated by the subcircular pit of the first lateral furrow. Palpebral lobe larger, higher, slightly farther back, eye ridge more prominent, and steeper slope of cheek behind palpebral lobe. Free cheek is like larger ones, except eye surface is farther forward.

With further increase in size (Pl. 24, figs. 2-4, 9) the main changes are widening and elevation of the lateral glabellar lobes so that they become fused outside the first lateral furrow, the

axial furrows stand higher, and thus the fixed cheeks slope less steeply inward. The eye lobe moves back, and the slope behind it becomes steep. Additional spines appear, and the larger ones are reduced to high tubercles. In cranidia of length (sag.) 1 to 2 mm. some 40 per cent of the specimens have the occipital spines diverging at less than 90° , whereas the remainder and all larger specimens have them diverging at 90° or more.

The close similarity between the development of the cranidium of *Calipernurus* and that of *Apianurus* is evident.

Pygidium: A transitory pygidium (Pl. 24, fig. 12) of Stage holaspis-1 has the first segment marked off by interpleural grooves, and the long pleural spines curve inward and backward. The pleural spines of the second segment are only slightly curved, and more inwardly directed. The posterior border bears three border spines. Axis of 3 rings, anterior with 2 pairs and a median spine, second two with one pair each. This specimen shows that the major pleural spines of the true pygidium correspond to the pleural spines of the thorax. Smaller transitory pygidia have not been recognized, but they would evidently be extremely similar to some of those here regarded as representing *Apianurus barbatus*, n.gen., n.sp. (Pl. 19, figs. 24, 25, 27-29). Small true pygidia (Pl. 24, figs. 8, 13, 14) have the additional pairs of border spines, though the anterior is extremely small.

Subfamily SELENOPELTINAE Corda, 1847

(=Selenopeltides Corda, 1847, p. 33, and Selenopeltidae
Prantl and Přibyl, 1949, p. 172)

Genus SELENOPELTIS Corda, 1847

Text-figure 25.

Synonym: *Polyeres* Rouault, 1847, type species by monotypy
P. dufrenoyi Rouault, 1847; see Clarke, 1892, p. 96; Prantl
and Přibyl, 1949, pp. 173-175.

Diagnosis: Cephalon transversely subrectangular in outline. Glabella gently convex, tapering slightly forward, occipital ring short (sag. and exs.), low median tubercle; wide fronto-median lobe, convex band across base; apparently three lateral glabellar lobes, defined by faint axial furrow, shallow first lateral and

deeper second lateral furrow, and by longitudinal furrow joining first lateral to occipital furrow, anterior part of this longitudinal furrow deep; basal lobe divided subequally by faint transverse furrow and posterior portion subdivided by longitudinal furrow. Inner corner of cheek inflated, merging into antero-lateral part of occipital ring. Crescentic eye lobe at about half length (exs.) of cheek and in inner part. Librigenal spine stout, long, directed upward and outward, no spines on anterior and lateral borders of cheek. Hypostome subrectangular in outline, wider than long, shallow median posterior notch, wide postero-lateral border; middle furrow broad, shallow, running in from antero-lateral corner of middle body. Thorax of 9 segments, axial rings with prominent lateral lobes, horizontal pleurae with ridge running in curve convex forward which distally runs out into long posterior pleural spine; anterior pleural spine downwardly and outwardly directed, curved. Pygidium with short axis and one pair border spines only, connected to first ring by prominent pleural ridge. External surface tuberculate or granulate.

Geological Range: Lower to Upper Ordovician.

Discussion: The peculiarities of this genus have long been recognized, and include the shortness of the occipital ring, the partial fusion of the basal and median glabellar lobes and subdivision of the former, the conspicuous lateral lobes of the thoracic axial rings, the forward curve of the main ridge of the pleura, and the lack of spines along the borders of the free cheek and pygidium (excepting the major pair). The anterior pleural spine was figured by Barrande (1852, Pl. 36. fig. 6; Pl. 37, fig. 25), and is curved, projecting downward and outward below the posterior pleural spine of the preceding segment.

Selenopeltis is here regarded as belonging within a separate subfamily (rather than family). I agree with Prantl and Přibyl (1949, p. 173) than *Selenopeltis* has affinities with the Mira-

Figure 25. *Selenopeltis buchi* (Barrande), Middle Ordovician, Bohemia. Approximately X $\frac{4}{5}$. A, cephalon, anterior view, based on MCZ 4317, Chlustina Beds, d_{62b}, "Brdatka" near Beraun. B, hypostome, exterior view, based on MCZ 4316, Drabov quartzites, d δ , Drabov. C, exoskeleton in dorsal view, based on MCZ 4319, Sárka Shales, d₇₁, Osek, MCZ 4316, MCZ 4317, etc.

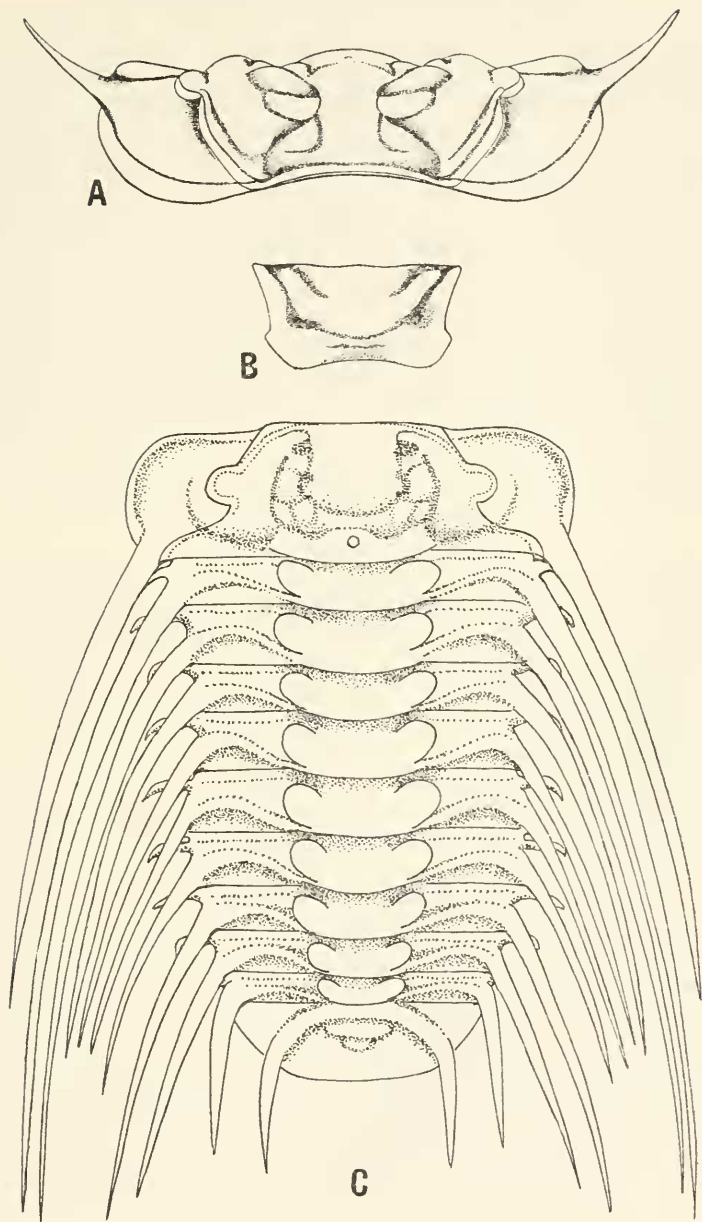


Figure 25

spinae rather than with other subfamilies, particularly in the general form of the cephalon, and notably the hypostome. But *Selenopeltis* shares many odontopleurid characters with other genera, and some of its peculiar features appear in these other genera. For example, *Dicranurus* also lacks spines on the lateral cephalic border; the curve of the pleural ridge in *Selenopeltis* is an accentuation of the same curve seen in such genera as *Miraspis* and *Dicranurus*; fusion of median and basal glabellar lobes occurs in *Apianurus*, n.gen.

Selenopeltis is well known from the Llanvirn to Ashgill of Bohemia, has been recorded in France, and more recently in Morocco (Termier and Termier, 1950, Pl. 194, figs. 1-4), and Shropshire (Whittard, 1952, p. 158), the latter in rocks of Arenig age.

Other Genera, Subgenera and Species Sometimes Referred to Odontopleuridae

Acidaspis ulrichi Bassler, 1919 (pp. 355-356, Pl. 37, figs. 6-8) is part of an Upper Cambrian trilobite (Wilson, 1952, p. 317), presumably the free cheek, and of unknown affinities.

Acidiphorus Raymond, 1925. Not an odontopleurid, probably a bathyrid (Whittington, 1953, p. 669).

Ancyropyge Clarke, 1892. Based on a pygidium, recently re-described (Stumm, 1953, p. 126, Pl. 6, figs. 1, 2), and may be an odontopleurid.

Bounyongia Etheridge and Mitchell, 1917, type species by monotypy *B. howningensis* Etheridge and Mitchell, 1917. Based on two poorly preserved specimens of the cephalon, one with a few thoracic segments attached, recently said by Gill (1948, p. 18) to be a subgenus which "must now lapse," since the character upon which it was founded — a pair of cephalic spines arising from the glabella — is a misinterpretation, the spines being occipital. Prantl and Přibyl (1949, p. 181) regarded *Bounyongia* as a synonym of *Ceratocephala*.

Glaphurus Raymond, 1905, and *Glaphurina* Ulrich, 1930. In 1913 Raymond (p. 723) placed the former genus in the Odontopleuridae, but later (1916, p. 138) thought it should be excluded. Hupé (1953, p. 229) comments on the apparent odontopleurid

characters. I consider the resemblance superficial, and agree with Hupé that these two genera may be placed in a separate family, allied to Telephidae (Hupé, 1953, pp. 228-230).

Globulaspis Reed, 1931, type species *Acidaspis* (*Globulaspis*) *prominens* Reed, 1931 (pp. 100-101, Pl. 5, figs. 5, 5a, 5b), from the Lower Silurian of southern Scotland. The holotype, the internal mould of an incomplete cranidium, appears to be unique. I do not think it shows much resemblance to *Whittingtonia*, as do Prantl and Přibyl (1949, pp. 133-134), and am not sure that it is an odontopleurid.

Pharostoma Corda, 1847, and *Ptychometopus* Schmidt, 1894, have sometimes been excluded with question from the Calymenidae, and comments have been made regarding their odontopleurid-like appearance (cf. Shirley, 1936, pp. 385-386; Öpik, 1937, p. 24). I consider this resemblance probably superficial, and that these genera belong with the calymenids (cf. Hupé, 1953, p. 232).

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